Sleeping trees and sleep-related behaviours of siamang (*Symphalangus syndactylus*) living in a degraded lowland forest, Sumatra, Indonesia.

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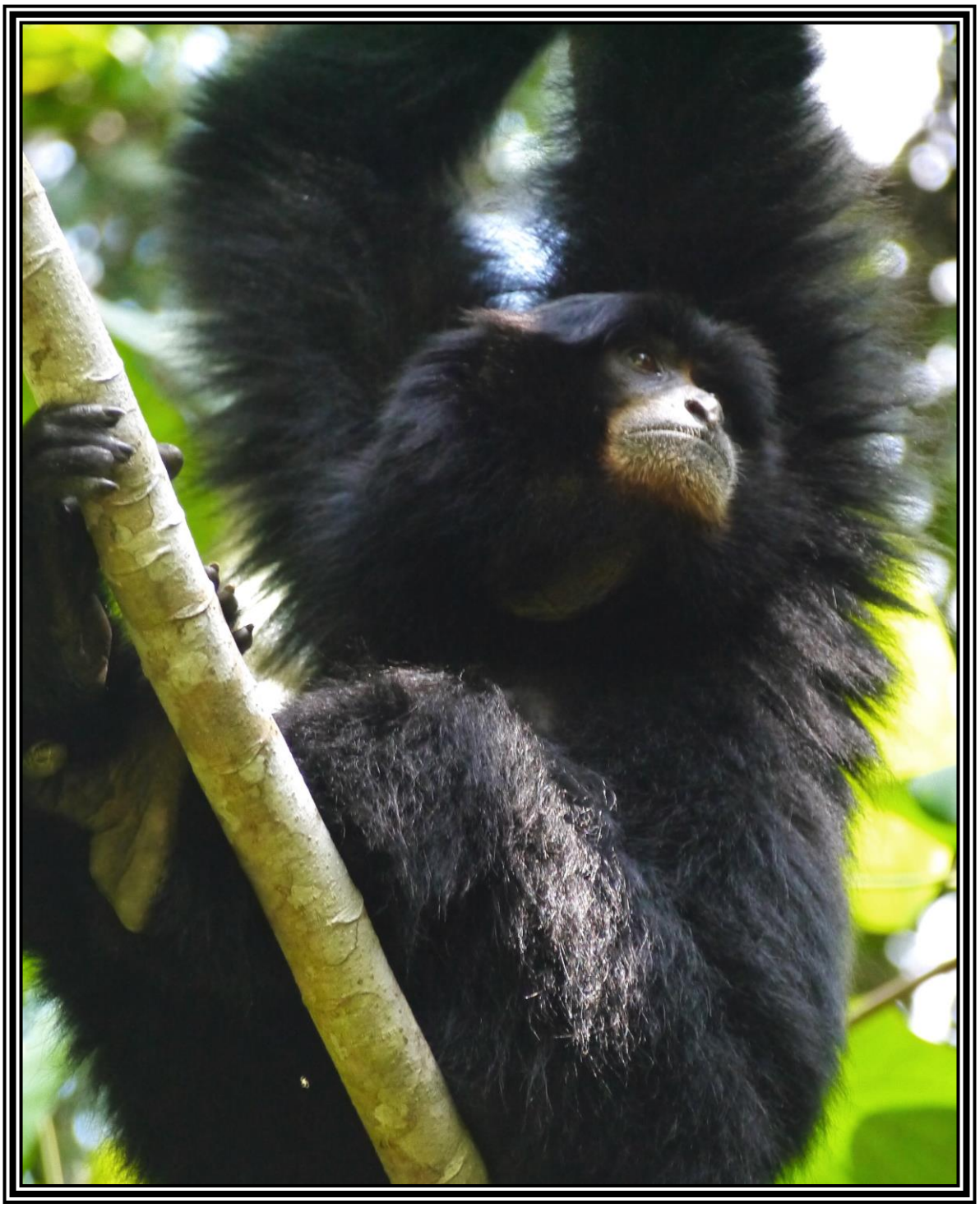

"In all works on Natural History, we constantly find details of the marvellous adaptation of animals to their food, their habits, and the localities in which they are found."

~ Alfred Russel Wallace (1835)

ABSTRACT

Tropical forests are hotspots for biodiversity and hold some of the world's most unique flora and fauna, but anthropogenic pressures are causing large-scale tropical forest disruption and clearance. Southeast Asia is experiencing the highest rate of change, altering forest composition with intensive selective and mechanical logging practices. The loss of the tallest trees within primate habitat may negatively affect arboreal primates that spend the majority of their lives high in the canopy. Some primate species can spend up to 50% of their time at sleeping sites and must therefore select the most appropriate tree sites to sleep in. The behavioural ecology and conservation of primates are generally well documented, but small apes have gained far less attention compared to great ape species. In this study, sleeping tree selection of siamang (*Symphalangus syndactylus*) were investigated from April to August 2018 at the Sikundur Monitoring Post, a degraded lowland forest in Gunung Leuser National Park, Sumatra, Indonesia. Siamang were shown to sleep at the end of branches in tall, stable, emergent trees, high above the mean canopy height. Sleeping trees had an optimum percentage of canopy connectivity and number of large branches, as well as being surrounded by taller trees. Siamang entered sleeping trees before sunset and left before sunrise. All these factors suggest that antipredation is an important factor affecting sleeping behaviour. However, siamang in this study had regular sleeping trees, a quality so far undocumented amongst other hylobatids. This re-use of the same sleeping trees goes against the idea that predation is the main driver of sleeping site selection, as regularly used sleeping sites are more predictable to predators. Sleeping tree re-use may be explained by the degraded nature of the Sikundur forest or could be an adaptation of the siamang's unique distribution, morphology and behaviour. Siamang did not position their sleeping trees close to fruiting trees but instead may select trees on a basis of comfort and

stability. By understanding siamang sleeping sites in greater depth, conservation management plans will be able to mitigate the loss of an already endangered primate species.

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1. INTRODUCTION

1.1 Overview

Tropical forests are hotspots for biodiversity and hold some of the world's most unique flora and fauna (Myers *et al*., 2000). Anthropogenic pressures are, however, causing large-scale forest clearance throughout the globe's biomes, removing valuable habitat for many endemic and endangered species (Brooks *et al*., 2002). Southeast Asia is experiencing the highest rate of deforestation, more so than that of South America (Wilcove *et al*., 2013). Forests are cleared with intensive logging practices for monoculture plantations (Koh & Wilcove, 2008; Wilcove *et al*., 2013). In Indonesia alone, only 3.8% of original primary forest remains (Cheyne *et al*., 2012). This alteration of land use not only changes the composition of vegetation, but also the ecosystem structure. Both intensive and selective logging practises alter the forests' arrangements by removing the largest and most commercially valuable trees (Priatna *et al*., 2006). Global demand for arboreal crops such as oil palm has also caused large-scale tropical forest clearance, resulting in huge reductions of orang-utan (*Pongo* spp.) numbers, for example, across Borneo and Sumatra (Estrada *et al*., 2017; Spehar *et al*., 2018). How forest degradation affects greater apes such as orangutans is well documented, but gibbons have been regarded as "the truly neglected ape", with historically far less research and conservation interest (Whittaker & Lappan, 2009). With better scientific understanding and relevant research it may be possible to understand the effects of habitat modification on small ape distributions, densities, and behaviours in greater depth.

There have been several studies to date that show primates select the tallest, most mature trees within their home range to sleep in (Whitten, 1982a; Tenaza & Tilson,

1985; Heymann, 1995; Reichard, 1998; Fan & Jiang, 2008; Phoonjampa *et al*., 2010; Cheyne *et al*., 2012; Fei *et al*., 2012; Caselli *et al*., 2017; Fei *et al*., 2017). As arboreal primates can spend up to 50% of their time at sleeping sites (*Hylobates albibarbis*, Cheyne *et al*., 2012; *Sapajus cay*, Smith *et al*., 2017), these trees are extremely important features in a their daily routine. Understanding how and why primates select sleeping sites and how the availability of sleeping sites across any given region may have been altered through human modification is therefore of conservation concern. The loss of the tallest and most commercially valuable trees could influence intra- and inter-species competition as a result. In addition, reducing the density of smaller surrounding trees may disrupt travel paths to sleeping sites. By studying the behaviours of primates it may be possible to make inferences about the evolution of human behaviours. It will also be scientifically useful and intrinsically valuable to know which trees and habitats are most favourable, leading to more efficient conservation management. Gibbons and siamang are small apes in the family Hylobatidae (Bartlett, 2007). They live exclusively in the canopy and are seldom seen coming to the ground. As arboreal primates, they spend the majority of their lives in the treetops and rely on certain tree characteristics to perform daily routine behaviours, such as foraging, travelling, socialising and resting (Gittins & Raemaekers, 1980). Removal of any type of tree that they depend upon may alter gibbon and siamang behaviour in one way or another, and has the potential to reduce fitness and ultimately cause extinction (Estrada *et al*., 2017; Smith *et al*., 2017). All 20 recognised species of gibbons are currently threatened with extinction (IUCN SSA, 2018), so understanding small ape habitat use and preference is of upmost conservation importance.

1.2 Sleep site selection in primates

Sleep is a fundamental behaviour demonstrated by all mammals but is particularly complex in primates given their dependence on cognitive processes and large brain sizes. Sleep contributes towards neurological processes, protein synthesis and energy conservation (Anderson, 1984; Campbell & Tobler, 1984; Walker & Stickgold, 2006). Sleeping sites are important as their abundance within the forest can ultimately affect an individual's reproductive success and impact survival rates (Lutermann *et al*., 2010; Phoonjampa *et al*., 2010; Cheyne *et al*., 2012). During sleep, individuals become less active and less aware of their surrounding environments, increasing the risks of predation (Lima *et al*., 2005). As a result, many behavioural strategies have evolved to offset this risk, such as group cohesion, vigilance, alarm calling, mobbing, cryptic behaviour, habitat selection and sleep site selection (Stanford, 2002; Ferrari, 2009; Hollén & Radford, 2009; Caselli *et al*., 2017).

Sleeping site studies are not uncommon within the literature, for example, how and why chimpanzees (*Pan troglodytes*) construct disposable one-use nests each night (Stewart *et al*., 2018). Great ape nests provide comfort and stability and may have limited importance for predator avoidance (Cheyne *et al*., 2013a). Nest building is rare in primates confined to instinctive behaviours in Prosimians and learned behaviours in great apes (Prasetyo *et al*., 2009). Instead, many other primate species opt for tree holes, caves or large emergent trees (Schmid, 1998; Qihai *et al*., 2009; Phoonjampa *et al*., 2010). Small apes (gibbons & siamang) are yet to be observed manipulating or constructing sleeping sites (Islam & Feeroz, 1992; Reichard, 1998; Fan & Jiang, 2008). Observations and studies show that they choose to sleep on bare branches, giving rise to several hypotheses as to why arboreal primates select specific trees to sleep in. This

includes anti-predator defence, food availability, thermoregulation, tree and branch stability and minimising parasite exposure (Pontes & Soares, 2005; Li *et al*., 2006; Franklin *et al*., 2007; Qihai *et al*., 2009; Cheyne *et al*., 2012; Fei *et al*., 2017). By choosing specific sleeping sites, individuals or groups can indirectly minimise the risk of detection and predation, as they become more inaccessible, more inconspicuous and less predictable (Anderson, 2000; Boinski *et al*., 2000; Caselli *et al*., 2017). This selection process allows primates to influence their own survival as well as overcoming any challenges they may face in their natural environment (Anderson, 1998; Reichard 1998; Fei *et al*., 2017).

Amongst the theories on sleeping site selection criteria, the most prevalent explanation for primate sleep site selection is the anti-predation strategy, as predators pose a serious threat to sleeping groups and individuals (Caine *et al*., 1992; Von Hippel, 1998; Di Bitetti *et al*., 2000; Liu & Zhao, 2004; Smith *et al*., 2007; Qihai *et al*., 2009; Duarte & Young, 2011; Barnett *et al*., 2012; Fei *et al*., 2017). As such, primates have evolved several behaviours to minimise the risk of detection and predation whilst sleeping. These include: selecting the tallest trees to sleep in (Whitten, 1982a; Reichard, 1998; Von Hippel, 1998; Di Bitetti *et al*., 2000; Fan & Jiang, 2008; Phoonjampa *et al*., 2010; Barnett *et al*., 2012; Fei *et al*., 2012; Cheyne *et al*., 2012; Feilen & Marshall, 2014; Fei *et al*., 2017); entering sleeping sites before nocturnal predators become active (Anderson, 1998; Reichard, 1998; Phoonjampa *et al*., 2010); irregularly using the same sleeping tree (Whitten, 1982a; Reichard, 1998; Von Hippel, 1998; Fan & Jiang, 2008; Phoonjampa *et al*., 2010; Cheyne *et al*., 2012; Fei *et al*., 2012; Teichroeb *et al*., 2012; Feilen & Marshall, 2014; Fei *et al*., 2017); moving rapidly into the sleeping tree, remaining quiet near or at the sleeping site (Reichard, 1998; Fan & Jiang, 2008; Qihai *et*

al., 2009; Xiang *et al*., 2010; Fei *et al*., 2012; Fei *et al*., 2017); defecating away from the sleeping site so that excreta do not attract predators; and moving away from the sleep site immediately after use (Reichard, 1998). Competition for these resources and thus for the best sleeping sites is therefore expected between and within primate species, with Tenaza (1975) observing larger primates evicting smaller ones from the best locations and into areas where they are potentially more vulnerable to predation. Studies of different aspects of sleep in primates are interesting and useful as they can indicate how species adapt to matters such as social relationships, staying fit and avoiding predators (Fan & Jiang, 2008). Given our evolutionary history, wider functionalities of primate sleep studies could possibly indicate how human behaviours evolved (Anderson, 1998).

1.3 Focus of study

The focus of this study is on wild siamang (Hylobatidae: *Symphalangus syndactylus*) living in a degraded lowland forest in Gunung Leuser National Park, Sumatra, Indonesia. Studies on hylobatid sleeping trees appear in the literature but are still relatively rare given the 20 species of small ape and around seven published research articles. Studies indicate that gibbons generally select tall, liana free, emergent trees with exposed crowns (Tenaza & Tilson, 1985; Phoonjampa *et al*., 2010; Fan & Jiang, 2008; Cheyne *et al*., 2012; Fei *et al*., 2012). Sleeping trees are rarely re-used and are often located near important food sources (Reichard, 1998; Phoonjampa *et al*., 2010; Fan & Jiang, 2008; Cheyne *et al*., 2012). Gibbons enter sleeping trees before sunset and leave after sunrise to reduce exposure to nocturnal predators (Tenaza & Tilson, 1985; Reichard, 1998; Fan & Jiang, 2008; Phoonjampa *et al*., 2010; Cheyne *et al*., 2012; Fei *et al*., 2012; Fei *et al*., 2017). It is unknown whether siamang will behave in a similar

manner or not due to their different morphology, behaviours and distribution amongst Hylobatidae.

This study is the first to assess sleeping behaviours and sleeping trees used by siamang, and how forest structure influences the decision. It is also the first sleeping site study to be undertaken on the island of Sumatra on any primate other than Sumatran orangutans (*Pongo abelii*; Sugardjito, 1983). Siamang are relatively unstudied within primatology considering their 'ape' status. Most published work on siamang comes from either southern Sumatra (O'Brien *et al*., 2003; Lappan, 2008) or the Malay peninsular (Chivers, 1974; Chivers, 1976; Gittins & Raemaekers, 1980), with little information on siamang living in Gunung Leuser National Park or the wider Leuser Ecosystem. Siamang are the only small apes to occur sympatrically with another gibbon species, which could have implications for their sleeping tree use and preference. As Sumatra's forests become more degraded, it is essential that research is undertaken into these behaviours in an aim to help preserve important primate habitat.

1.4 Hylobatid sleep site selection

There has been a growing interest in sleeping site selection of hylobatids, with previous studies indicating species prefer tall trees that emerge above the mean canopy height (*Hylobates klossi*, Whitten, 1982a; *Hylobates lar*, Reichard, 1998; *Nomascus concolor jingdongensis*, Fan & Jiang, 2008; *Hylobates pileatus*, Phoonjampa *et al*., 2010; *Nomascus nasutus*, Fei *et al*., 2012; *Hylobates albibarbis*, Cheyne *et al*., 2012; *Hoolock tianxing*, Fei *et al*., 2017). As well as offering a platform for pre-dawn singing, the principal hypothesis behind this selection is security from terrestrial predators (Whitten 1982a; Whitten 1982b; Anderson, 1984). Additionally, the positioning of feeding trees,

tree and branch stability, and the presence of neighbouring groups may also influence sleeping site selection (Phoonjampa *et al*., 2010). Orangutans have more freedom when selecting sleeping sites, as their larger body sizes means that they are less vulnerable to predation, giving potential for inter-specific competition with gibbons and siamang for the best arboreal sleeping sites (Cheyne *et al*., 2012). However, Chetry *et al*. (2008) have shown that competition between species has been avoided in five sympatric species in Assam, India. Three species of macaque (*Macaca mulatta*, *Macaca arctoides* & *Macaca leonina*), one langur species (*Trachupithrcus pileatus*) and one gibbon species (*Hoolock hoolock*) all occupy the same habitat but select different trees to sleep in, avoiding any conflict (Chetry *et al*., 2008). The effects of temporal changes in microhabitat can also influence sleeping site selection. The western hoolock gibbon (*Nomascus concolor*) was shown to reside in sleeping trees nearer to villages and cultivated land on the forest edges when food availability became scarce in the forests interior (Ni *et al*., 2017). Additionally, the removal of sleeping trees (as well as feeding trees) reduces the quality and area of pristine gibbon habitat. As such Western hoolock gibbons (*Hoolock hoolock*) in the Assam region of India have been observed moving towards human settlements in search of isolated forest patches (Das *et al*., 2009).

Phoonjampa *et al*. (2010) determined that the most influential factor in sleeping site selection of pileated gibbons' (*Hylobates. pileatus)* was predator avoidance, however, other non-mutually exclusive factors also played a part. Results revealed sleeping sites were chosen near, but not in, their last feeding tree and that sites where other pileated gibbons' ranges overlapped were avoided (Phoonjampa *et al*., 2010). Reichard's (1998) study of lar gibbons (*Hylobates lar*) came to a similar understanding, concluding that the number of safe sleeping places may not be limited, and once safe sleeping sites are

identified, additional criteria may support the final decision (Reichard, 1998). Additionally, Kloss gibbons (*Hylobates klossi*) avoided using trees with vines and lianas due to the presence of ant colonies (Whitten, 1982a), and such structures may also provide easier access for pythons or humans as potential predators (Tenaza & Tilson, 1985; Cheyne *et al*., 2012). Yunnan black crested gibbons (*Nomascus concolor jingdongensis*) also selected the thickest, tallest trees with the largest crowns and slept on the steep slopes of branches near important food sources. It was concluded that these sites were chosen to make detection and approach by predators more difficult and escape routes easier in the dark (Fan & Jiang, 2008). Interestingly, the gibbons also huddled together during cold nights and at higher altitudes in response to the lower temperatures to aid thermoregulation (Fan & Jiang, 2008). Cao Vit gibbons (*Nomascus nasutus*), however, did not select lower elevation sleeping sites during colder months to minimise thermoregulatory stress, and slept in trees more than 100m away from food sources, rejecting those potential hypotheses (Fei *et al*., 2012). Instead, as with the other gibbon species, their selection of sleeping sites correlated the most strongly with the predation avoidance hypothesis (Fei *et al*., 2012).

The most recent study of sleeping site selection in gibbons was carried out in the newly described Skywalker hoolock gibbon (*Hoolock tianxing*) by Fei *et al*. (2017), and supporting said notions that sleep site selection is dependent on the anti-predation theory for several reasons. The gibbons rarely re-used sleeping trees on consecutive nights and over the period of the study slept in dozens or even hundreds of trees depending on the focal group. They moved quickly and directly into the sleeping trees, on average less than 2.5 hours before sunset and remained relatively quiet and still once they had settled. It is thought that this is to reduce the risk of being detected by

nocturnal and dusk foraging predators (Anderson, 1998; Reichard, 1998; Fan & Jiang, 2008; Phoonjampa *et al*., 2010; Fei *et al*., 2012; Fei *et al*., 2017). Skywalker hoolock gibbons selected the tallest trees with the lowest branches at around 10 metres high, choosing to sleep on small braches near to the top of the tree. This is thought to keep distance and detection by terrestrial predators to a minimum, but also reduces the risk of attack from the air. Fei *et al*. (2017) concluded that sleep site selection in *H. tianxing* corresponds to the avoidance of predators, as perceived by similar studies carried out on other gibbon species (Whitten, 1982a; Reichard, 1998; Fan & Jiang, 2008; Fei *et al*., 2012; Cheyne *et al*., 2013b; Fei *et al*., 2017). Tilson and Tenaza (1982) showed that the Mentawai Island langur (*Presbytis potenziani*) and Kloss' gibbon (*H. klossii*), who both occupy overlapping home ranges, select large emergent trees to sleep in, with gibbons opting for vine and liana free trees, whilst langurs did not (Tilson & Tenaza, 1982; Anderson, 1998). Subsequently, the number of langurs killed by predators, including human hunters, was disproportionately higher, as access to higher branches was more achievable by climbing lianas. This indicates that inter-specific competition for sleeping sites can negatively influence population numbers of the subordinate species.

Previous studies strongly suggest that predator avoidance is the principal driving force in gibbon sleeping site selection, however, a multitude of factors may influence the final decision (Table 1.1). Avoiding predators seems a reasonable life history strategy in this respect, as failure to do so may result in the ultimate price, i.e. death and a complete loss of fitness (Cheyne *et al*., 2012). As anthropogenic disturbances remove valuable habitat at an ever-increasing rate, it is important to identify the trees and habitats that gibbons select for sleeping behaviours to avoid reduced and fragmented populations, or even extinction.

Table 1.1 Summary of previous studies of hylobatid sleeping sites focusing on tree characteristics and gibbon behaviours. 'n/a' indicates that this variable was not considered part of that particular study.

Species	Selected tall trees?	Use many sleeping trees?	Avoided food sources?	Avoided lianas & vines?	Thermo-regulation behaviours?	Overlapping sleeping ranges?	Inconspicuous* behaviour at sleeping site
Kloss gibbon *Hylobates klossii*	Yes	Yes	n/a	Yes	n/a	n/a	n/a
Lar gibbon *Hylobates lar*	Yes	Yes	Yes	No	No	Yes	Yes
Pileated gibbon *Hylobates pileatus*	Yes	Yes	Yes	Yes	n/a	No	n/a
Yunnan black crested gibbon *Nomascus concolor jingongensis*	Yes	Yes	No	Yes	Yes	n/a	Yes
Cao Vit gibbon *Nomascus nasutus*	Yes	Yes	Yes	Yes	No	No	Yes
Skywalker hoolock gibbon *Hoolock tianxing*	Yes	Yes	No	n/a	n/a	n/a	Yes
Agile gibbon *Hylobate albibarbis*	Yes	Yes	Yes	Yes	n/a	n/a	Yes

*Enter sleeping trees before sunset/leave after sunrise. Remain still and quiet at sleeping site

1.5 Research aims, objectives and hypotheses

The aim of this study is to understand which vegetation characteristics determine a sleeping tree and whether the surrounding forest's structure influences this decision in siamang. Understanding the fundamental relationships species have with their surrounding environs will help identify the most favourable trees and habitats within the area. This will allow recommendations to be made on more efficient conservation management strategies for the tropical lowland forest at Sikundur, and for wider areas on Sumatra. By understanding siamang sleeping behaviours in greater depth, it may be possible to understand the evolutionary life strategies of hylobatids throughout Asia, and possibly primate species around the globe.

This study's objectives and predictions are:

- **Objective 1:** To identify which characteristics are selected as sleeping trees by siamang, compared to similarly tall trees that are not selected as sleeping trees, including identifying the characteristics of surrounding trees.
    - **Hypothesis 1a:** Siamang will select tall, liana free, emergent trees as sleeping sites with exposed crowns and an optimum number of stable branches and canopy connectivity.
    - **Hypothesis 1b:** Sleeping trees will be surrounded by taller, more stable trees compared to control trees that are not selected as sleeping trees.
    - **Hypothesis 1c:** Groups of siamang will be more selective in their sleeping tree choice than a solitary individual. Groups will require larger, more stable trees to support them.

- **Objective 2:** To observe the behaviours of siamang in combination with objective 1 to ascertain whether siamang select sleeping trees based on predator avoidance, tree and branch stability/comfort or distance to food resources.
    - **Hypothesis 2a:** Siamang will select sleeping trees based on a predator avoidance theory.
        - **2ai:** They will avoid frequently re-using the same sleeping trees, especially on consecutive nights.
        - **2aii:** They will move into sleeping trees before sunset and move away before sunrise.
        - **2aiii:** They will sleep at the end of branches, high above the mean canopy height.

- **Hypothesis 2b:** Siamang will select sleeping trees based on a resource theory. They will sleep in close proximity to important food sources (fruiting trees).
- **Hypothesis 2c:** Siamang will select sleeping trees based on a comfort and stability theory. These trees will provide a better quality of sleep to optimise time budget behaviours the next day.

- **Objective 3:** To determine whether there is inter- and intra- competition. This will be achieved by mapping siamang home ranges and the location of sleeping trees within these ranges.
  - **Hypothesis 3a:** Siamang sleeping trees will be in the core areas of their ranges to reduce competition with neighbouring groups. Sleeping trees will therefore not be in over lapping areas.
  - **Hypothesis 3b:** Inter-species competition is expected as multiple arboreal primate species live in the area but will be indirect if observed (i.e. other species using a siamang sleeping tree when they are in another sleeping tree).

2. BACKGROUND

2.1 Importance of primate conservation

Tropical forests are being removed at an unprecedented rate. Since 1990 around 129 million hectares of forest, an area roughly the size of South Africa, has been lost due to human activities (FAO, 2015). As a consequence, valuable carbon stores have been disturbed, affecting the carbon cycle, which has ultimately increased global temperatures. This disruption and loss of important habitat requires immediate scientific research if we are to better understand how species such as primates adapt to these changes within their ecosystem. With larger body sizes, slower life histories and limited dispersal ability primates can be sensitive to small changes within their habitats (Korstjens & Hillyer, 2016). This makes them good focal species for measuring response to environmental changes, with primate distributions correlating well with those of other mammal species (Emmons, 1999). Primates are however, popular within community science and respond well to publicity, making them important flagship species for conservation campaigns and eco-tourism. Out of the 435 extant primate species listed on the IUCN Red List, 83 are listed as Vulnerable, 121 Endangered and 63 Critically Endangered (IUCN, 2017a), indicating that over half of the world's primate species are at risk of extinction. Conservation of primate populations would therefore be beneficial, not only for the focal subjects but also for the target habitat, as well as the forest ecosystem and the species that dwell within it.

2.2 Biodiversity hotspots

There have been five periods in earth's history (Ordovician, Devonian, Permian, Triassic & Cretaceous) where mass extinction has caused large-scale species declines across the globe. Biologists have suggested that a sixth mass extinction event is now

underway through anthropogenic means, and efficient conservation strategies are desperately needed (Barnosky *et al*., 2011). On average each year, around 52 species of mammals, birds and amphibians move one category closer to extinction, most notably due to habitat loss, climate change, overexploitation and economic gain (Hoffman *et al*., 2010; Ceballos *et al*., 2015). With the current rate of biodiversity loss, humans, within as little as three lifetimes, will be deprived of ecosystem services and ecological functioning that many species provide (Ceballos *et al*., 2015).

As such, an effective way to save the most species per dollar invested is to identify the areas in greatest need, where the payoff of protection would be the highest (Myers *et al*., 2000). Biodiversity hotspots have thus been identified where regions of increased species richness and species endemism have incurred a loss of more than 70 per cent of the original primary vegetation (Myers *et al*., 2000). Twenty-five hotspots were initially identified (Myers, 1988), with an additional ten terrestrial regions and ten marine biodiversity hotspots globally recognised post revisions (Roberts *et al*., 2002; Pilgrim *et al*., 2005; Mittermeier *et al*., 2011; Hopper *et al*., 2016) (Fig. 2.1).

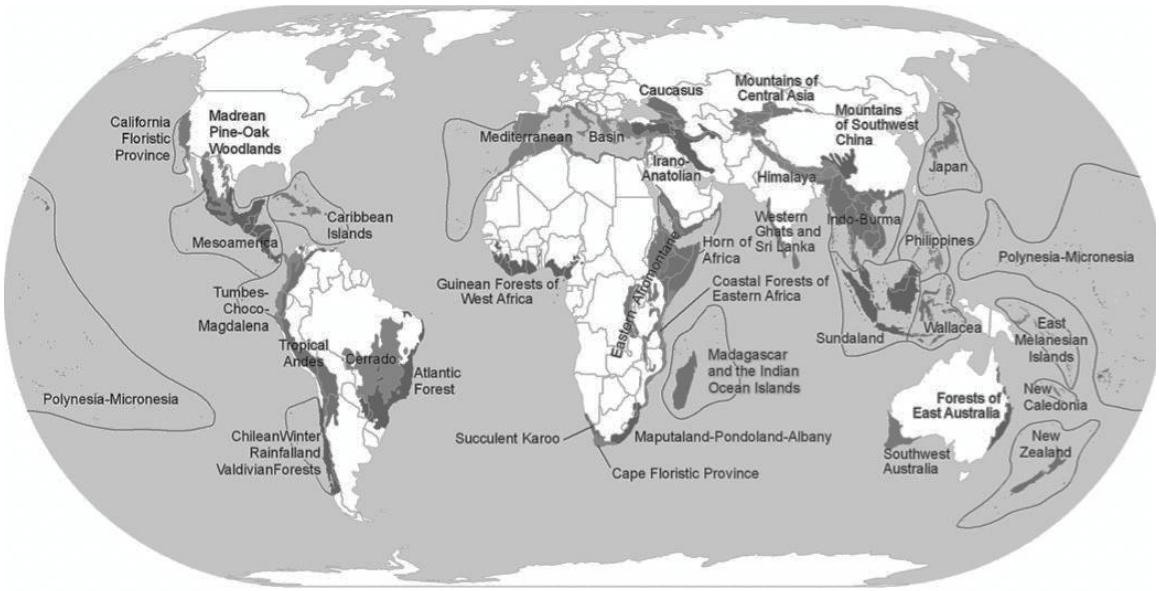


Figure 2.1 Global Biodiversity Hotspots (Mittermeier *et al*., 2011) showing Earth's 35 most biologically rich and threatened terrestrial ecosystems.

Southeast Asia contributes to four of these biodiversity hotspot regions: Indo-Burma; Philippians; Wallacea and Sundaland (Mittermeier *et al.,* 2011). The historical fluctuating sea levels have allowed current islands located within the Sundaland region such as Sumatra, Borneo and Java to become separated and reconnected to mainland Asia repeatedly throughout the Pleistocene glacial episodes (Jablonski, 1993; Mittermeier *et al.,* 1999; Sodhi *et al.,* 2004). This continually allowed for speciation events when sea levels rose and biotic migration when sea levels dropped (Meijaard, 2004; Sodhi *et al.,* 2004). As a consequence, the Sundaland region now holds the fourth greatest total number of endemic vertebrate taxa worldwide (Mittermeier *et al.,* 1999), with around 40% of all mammal species endemic to the area (Sodhi *et al.,* 2004).

2.3 Deforestation in Southeast Asia

In Southeast Asia, tropical forests play vital roles in environmental protection and provide socio-economic benefit on a local scale, but globally they are an important carbon store (Lee, 2009; Stibig *et al*., 2013). Carbon released into the atmosphere as a result of deforestation is a major contributor to global climate change (Dennis *et* al., 2005; Sheil *et* al., 2009; Miettinen *et al*., 2011). Even though this kind of deforestation is restricted to the tropics, the affect it has environmentally, economically and politically can be felt on a global scale (Miettinen *et al*., 2011). Deforestation on islands within the Sundaland region is of highest concern with Hansen *et al.* (2009) estimating that Indonesian forest cover declined at a rate of 1.5% per year between 1990 and 2000. Additionally, there was a 70% loss (approx. 773,000 km²) of the original lowland forest cover by 2010, as well as 65% loss (approx. 96,000 km²) of peat swamp forests (Wilcove *et al*., 2013). Oil palm production is the main cause of this clearance (Koh & Wilcove, 2008), but it is not the only driving force. As the requirement for pulp, paper

and rubber grows, more forest is cleared for plantations to meet these demands (Wilcove *et al*., 2013). As such, only 3.8% of Indonesia's forests are now classified as 'primary' (Cheyne *et al*., 2012).

2.4 Sumatra

Sumatra, a large elongated island that forms part of western Indonesia in the Sundaland region, has recently gained renewed global interest because of its high carbon stores, high biodiversity-rich lowland forests, as well as its increasingly high deforestation rates (Page *et al.,* 2002; Indonesia, WWF, 2008; Gaveau *et al.,* 2009). Between 1985 and 1997, the island incurred 6.7 million hectares of forest loss, putting the effectiveness of protected areas into question (Gaveau *et al*., 2007). This has, however, not reduced the rate at which forests are cleared to make way for more palm oil plantations, pulp and paper plantations, and logging and coal mining, with an additional 8.2 million hectares cleared between 2000-2010 (Abood *et al*., 2015). This loss contributed to around 56% of the total loss of forest cover in Southeast Asia (Stibig *et al*., 2013). Nevertheless, Sumatra still hosts some of the world's richest and most diverse ecosystems on the planet, providing ecosystem services and livelihoods to millions of people (WWF, 2017). The island is home to over 10,000 plant, 201 mammal and 580 bird species (Whitten *et al*., 2000; Margono *et al*., 2012). Two and a half million hectares of protected National Parks are spread across three distinct locations: Kerinci Seblat National Park; Bukit Barisan Selatan National Park and Gunug Leuser National Park (UNESCO, 2017).

2.4.1 Leuser Ecosystem

In northern Sumatra, across the Acehnese and North Sumatra border lies the Leuser Ecosystem, a 26,000km² expanse, described as one of the "World's Most Irreplaceable Protected Areas" – it is the last known place on earth where elephants (*Elephas maximus sumatranus*), rhinos (*Dicerorhinus sumatrensis*), tigers (*Panthera tigris sumatrae*) and orangutans (*Pongo abelii*) coexist (Le Saout *et al*., 2013; Schwitzer *et al*., 2015). Despite a National Park status and the surrounding Leuser Ecosystem buffer zone, the threat of deforestation is widespread throughout (Sloan *et al*., 2018), even though the local community strongly rely on its ecological and economic value.

Van Beukering *et al.* (2003) estimated that the economic value of Leuser in a complete conservation scenario over a 30-year period would be $9.5 billon USD. This is $2.5 billon USD more than if the area was completely logged and slightly higher if a selective utilisation scenario was adopted ($9.1 billon USD). This demonstrates that the economic value of Leuser is worth protecting for water supply, flood prevention, tourism, biodiversity and agriculture than timber and oil palm plantations would ever be worth. More recent developments threaten the landscape with unofficial roads not observed on government maps and planned infrastructure such as power stations and power lines, contradicting national conservation strategies (Sloan *et al*., 2018).

The Leuser Ecosystem has recently gained international headlines. In March 2017, Indonesia's Ministry of Energy and Mineral Resources declined a permit for PT Wanyan Mining Gayoindo within the Leuser Ecosystem, a mining project owned by Chinese investors that has engaged in conflict with Aceh villagers for the past eight years. The decision to decline the permit due to paper work not being submitted on

time, will alleviate pressures on the local Gayo tribe – an indigenous group of the Ache highlands (Mongabay, 2017a). Additionally, three months later a moratorium was declared by the Acehnese government banning land clearance for oil palm plantations by companies, even if they already had a licences to develop. This comes after HAkA (the local Forest, Nature and Environment of Aceh watchdog) unveiled 3,941 hectares of forest had been removed since January 2017 (Mongabay, 2017b). These steps taken by the local authorities show the world how important this protected area is and what the true economic value can be.

2.4.2 Sikundur

A relatively unstudied site located in the Langkat District of North Sumatra known as the Sikundur Monitoring Post (an area 7x15km within the Leuser Ecosystem and Gunung Leuser National Park) has been the focal point of recent conservation studies given the presence of large Southeast Asian mega fauna (Knop *et al.,* 2004; Hitchcock & Meyers, 2006; Nowak, 2013; Alexander *et al*., 2018). Since occupation by the Sumatran Orangutan Conservation Programme (SOCP) in 2013, there has been a permanent surveillance team at Sikundur monitoring the behaviour and distribution of orangutans for research and conservation purposes (Nowak, 2013). This has opened the gateway for other research teams and universities to expand their investigation of a range of species, particularly primates. Sikundur is a degraded dipterocarp lowland and alluvial forest that was mechanically and selectively logged from the 1970s to the 1990s but has since been left to naturally recover (de Wilde & Duyfjes, 1996). As well as siamang, Sikundur's primates include one other hylobatid, the white-handed lar gibbon (*Hylobates lar*), two species of macaque (*Macaca nemestrina* & *Macaca fascicularis*),

Thomas' langur (*Presbytis thomasi*), the Sunda slow loris (*Nycticebus coucang*) and the critically endangered Sumatran orangutan (*Pongo abelii*).

2.5 Hylobatidae

The family Hylobatidae, commonly known as gibbons, are small apes within the Primate Order. Found throughout tropical and subtropical South and Southeast Asia, there are up to 20 extant species represented across four genera: *Hoolock* (hoolock gibbons); *Nomascus* (crested gibbons); *Hylobates* (lar & dwarf gibbons) and *Symphalangus* (siamang; Mittermeier *et al*., 2013; Fan *et al*., 2107; Gibbon Research Lab, 2017). As arboreal primates, gibbons use brachiation, the use of forelimbs to swing between trees and branches, as their primary mode of locomotion (Fleagle, 1976; Gittins, 1983; Cannon & Leighton, 1994; Fan *et al*., 2013; Fig 2.2). Unlike other apes, gibbons do not build nests, and instead rest by sitting or lying on branches without modifying their surrounding environment (Reichard, 1998; Cheyne & Brulé, 2004; Cheyne, 2010; Cheyne *et al*., 2012). Usually living in small groups of two to six individuals (Reichard, 1998), they exhibit mostly monogamous mating systems and produce loud song bouts to maintain relationships and defend their territories (Geissmann, 1999). Three species of hylobatid occur on the island of Sumatra: *Hylobates lar* (lar gibbon), *Hylobates agilis* (agile gibbon) and *Symphalangus syndactylus* (siamang; the focus of this study). Whilst lar gibbons and agile gibbons occupy different geographic ranges, siamang occur sympatrically with both and co-exists with lar gibbons in northern Sumatra and southern Malaysia, and with agile gibbons in central and southern Sumatra and a small region on the Malay peninsula (Fig. 2.3).

2.5.1 Siamang (Symphalangus syndactylus)

Classified as endangered on the IUCN Red List (IUCN, 2017b), siamang are the only species of gibbon to occur sympatrically with other gibbons throughout their home ranges (Fig. 2.2). They are the largest member of Hylobatidae, almost twice the size of most other gibbons, weighing 10-12kg (Reichard & Preuschoft, 2016). Siamang are distinctively different from other gibbon species as the second and third digit on their feet are partly joined by connective tissue, hence the name *Symphalangus syndactylus*, "united fingers" in Ancient Greek (Gibbon Research Lab, 2017). Another distinguishing feature is their large gular throat sac, found in both sexes, which aids in producing loud, resonating calls throughout the forest (Gittins & Raemaekers, 1980). There is no dimorphism between males and females and all ages display jet-black fur colouration (Fig. 2.4).

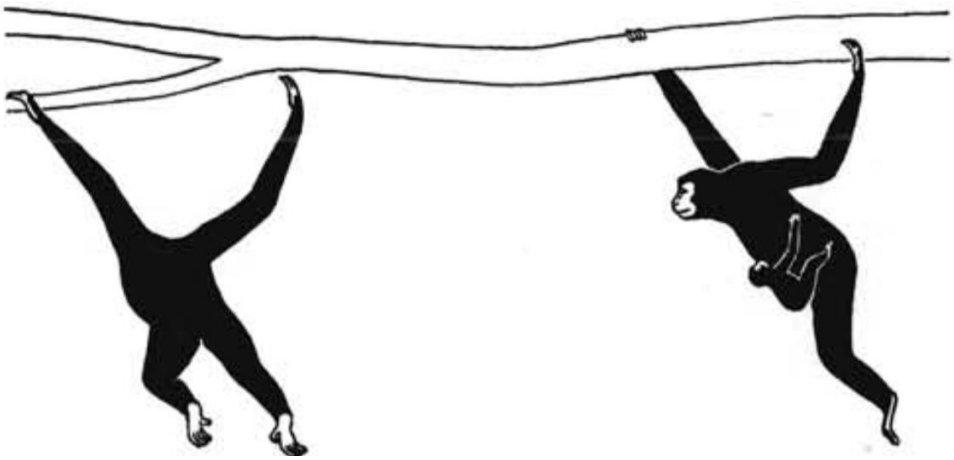


Figure 2.2 Siamang brachiating along a branch. Adapted from Fleagle (1974).

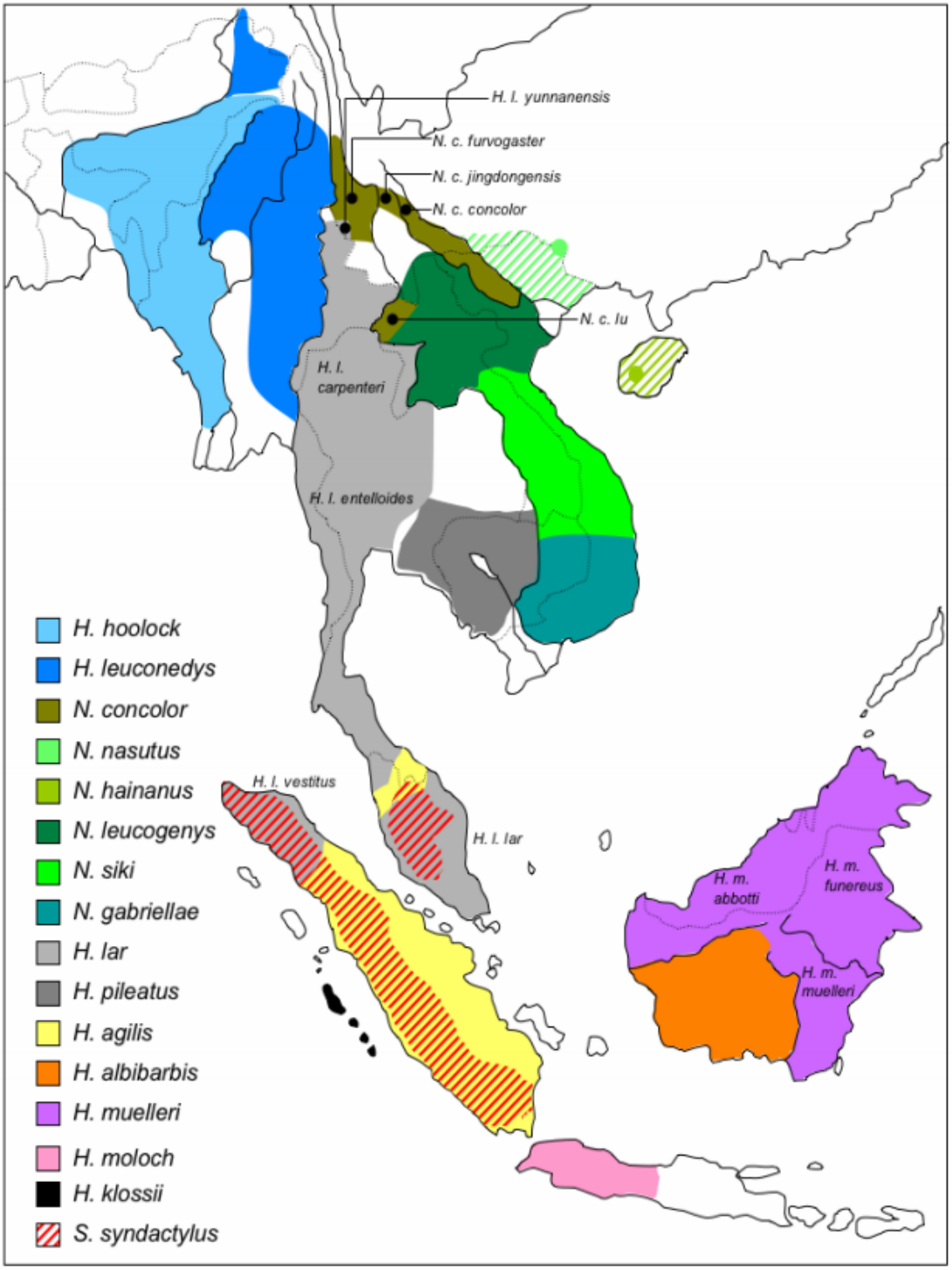


Figure 2.3 Geographical distribution of gibbons available in Mootnick *et al*., 2010. Dotted lines represent country borders, solid lines represent major rivers. Hatched distribution of *N. nasutus* and *N. hainanus* are historic ranges. Hatched distribution of *S. syndactylus* shows sympatric habitat range with *H. lar* and *H. agilis* on the Malay peninsula and Sumatra. Note that the number of species is different to current day counts, as new descriptions have been made. The smaller, more northern range of *H. leuconedys* is now considered a separate species (*H. tianxing*). *N. annamensis* has been classified as a separate species to *N. gabriellae*. *H. m. funereus* and *H. m. abbotti* are now considered separate from *H. muelleri*.

Figure 2.4 Male and female siamang groom one another. They are almost identical in shape, size and colouration (Photo: N.Harrison).

2.5.2 Home ranges, group sizes and population densities

The behavioural ecology for siamang has been previously documented in the literature but more focus has been placed on populations from the Malay peninsula and southern Sumatra. These studies reveal siamang have a home range between 15-48 hectares (Chivers, 1974), with daily range lengths of around 1km per day (Gittins & Raemaekers, 1980). Mean group sizes for siamang are at three individuals per group (MacKinnon, 1978), with population densities estimated specifically at Sikundur to be 0.40 – 2.11 groups/km^2 (Hankinson, 2017).

2.5.3 Feeding habits

Home ranges, mean group sizes and population densities are most likely driven by food resources. When fruit is abundant, the siamang diet can comprise of up to 90% fruit, shifting to young leaves, shoots, flowers and insects when fruit is less widely available or there is more competition for resources (Bartlett, 2007; Cheyne, 2010; Barlett & Light, 2017). Generally, siamang are less frugivorous than other species of gibbons, where fruit makes up around 30% of the siamang diet, compared to lar gibbon and agile gibbon, of which fruit compromises around 50% and 60%, respectively (Gittins & Raemaekers, 1980).

2.5.4 Sleeping habits

Siamang are cohesive within their groups and display synchronised behaviours in their sleeping habits, where all members of the group sleep in one or two adjacent trees (Gittins & Raemaekers, 1980). In comparison, individuals of groups of lar gibbons have been observed to sleep in separate trees, often scattered over 100m (Gittins & Raemaekers, 1980). Gittins & Raemaekers (1980) also document that sleeping takes place high up in the canopy for siamang, most likely for predator avoidance.

2.6 Overview of the literature

Deforestation and the removal of both the largest and most valuable trees and the surrounding vegetation could negatively impact primate habitat and the behaviours species exhibit within it. In a world where pristine, undisturbed tropical forests are becoming increasingly sparse, it is vital to understand how species respond to environmental changes. Primates are highly specialised mammals, which have evolved a range of specific behaviours over many thousands of years (Chazdon *et al*., 2009). If

important primate habitat is lost, not only do populations become more fragmented and isolated, individuals and groups may suffer a loss of fitness from not being able to exhibit behaviours relating to their surrounding environs.

Primates spend up to 50% of their time at sleeping sites (Cheyne *et al*., 2012; Smith *et al*., 2017), where they become less active and less aware of the risks around them, increasing opportunities for predators (Lima *et al*., 2005). Sleeping site selection studies are not novel within primatology, and previous investigations have revealed that the most widespread theory as to why arboreal primates chose specific sites to sleep is for predator-avoidance (Whitten, 1982a; Whitten, 1982b; Anderson, 1984), although other factors may affect the final decision. Information on hylobatid sleeping site selection is available throughout the literature, however, there is little or no information on siamang sleeping behaviours or sleeping trees, and a study of this kind is yet to be conducted on Sumatra.

More detailed research into sleeping site selection of siamang as well as other arboreal primates on Sumatra would assist in identifying the trees and habitats, which species rely upon daily. From this it will be possible to aid protection of remaining primary forests, as well as assisting conservation management plans of any regenerating forests that may act as a corridor between isolated patches. Action plans such as this will not only assist in ensuring the preservation of the focal species for future generations, but will provide protection and hope for other forest dwelling species. Finally, by expanding current knowledge of sleeping site selection and forest structure requirements, it may be possible to provide an insight into the evolution of human behaviours.

3. METHODS

3.1 Study site

This study was carried out at the Sikundur Monitoring Post within the Gunung Leuser National Park, GLNP (Taman Nasional Gunung Leuser, TNGL; Fig. 3.1) and within the Leuser Ecosystem (04°58'- 04°59' N, 98°04'- 98°05' E), Sumatra, Indonesia. Whilst the majority of TNGL and Leuser Ecosystem lie in Aceh, Sikundur is part of the Sumatera Utara province (North Sumatra). All fieldwork was carried out from 26th April 2018 to 10th August 2018 by NJH and one local field assistant (Ucok Sahrizal) who had extensive experience in following siamang and of the Sikundur forest. The site rises 30-100m above sea level and is comprised of a series of man-made trails through dipterocarp lowland forest and accompanying alluvial forest (Knop *et al*., 2004; Fig. 3.2). Throughout its history it has been mechanically and selectively logged on both small and large scales from the 1970s to the 1990s but has since been left to recover naturally (de Wilde & Duyfjes, 1996; Nowak, 2013). Logging, however, still occurs in the protected areas with the largest and most commercially valuable trees being felled illegally (Priatna *et al.*, 2006), as well as tree removal along the rivers and small areas cleared for plantations (Fig. 3.2). As such, the site offers the opportunity to study how different species are responding to anthropogenic disturbance across habitat types.

Between April and August 2018, mean temperatures were recorded at 27.2°C (min = 20.8°C, max = 38.9°C), with monthly rainfall at 251.4mm (min = 151mm; max = 396.3mm), making it a model climate for a diverse range of life. There are two seasons in Sumatra, one being a drier period between May and September, with the wet season beginning in the northern part of Sumatra in October.

Figure 3.1 The location of the Sikundur Monitoring Post in relation to the Leuser Ecosystem and the Gunung Leuser National Park, available in Nowak (2013).

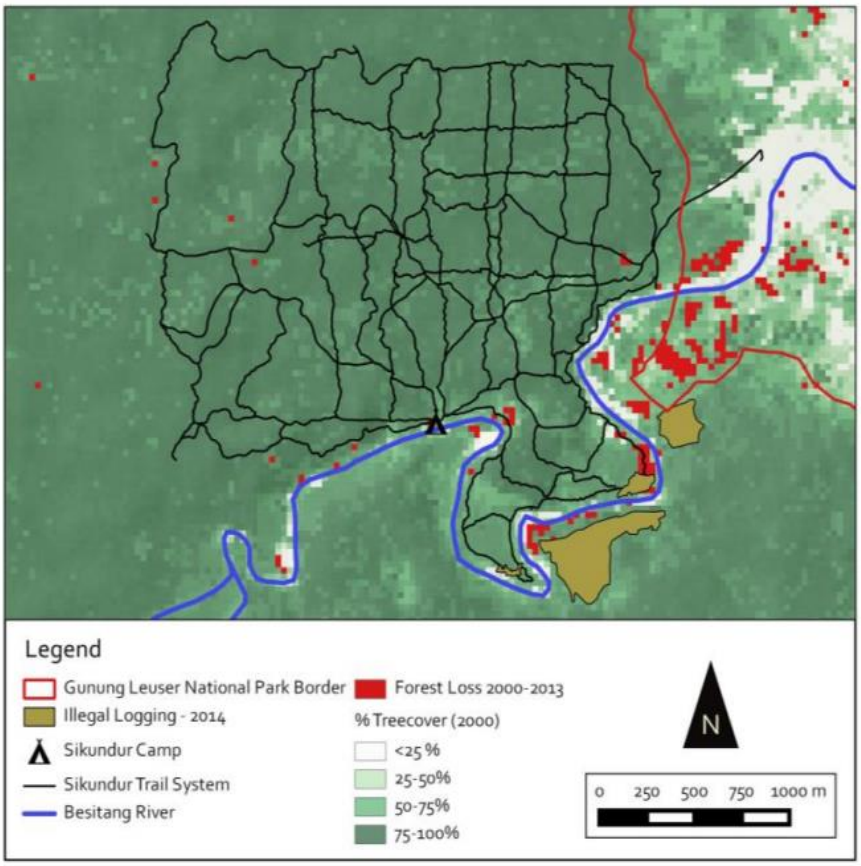


Figure 3.2. Man-made trails and recent illegal logging at the Sikundur Monitoring Post, available in Nowak (2013).

During the study, camera traps identified that large and medium-sized predators such as Sumatran tigers (*Panthera tigris sumatrae*), clouded leopards (*Neofelis diardi*), and leopard cats (*Prionailurus bengalensis*) are still present in the area and should be considered potential predators of siamang. Aerial predators also pose a potential threat, especially to younger, smaller individuals and the perception of risk was documented when a white-bellied sea eagle (*Haliaeetus leucogaster*) circled overhead and the siamang ceased all conspicuous behaviour until the bird was no longer visible.

3.2 Study individuals

To maximise the understanding of sleeping tree use, one group of siamang (Group A) and one solitary female (Group B) were followed during the study period. Group A was

a family unit consisting of one adult male, one adult female and their sub-adult male offspring. In June 2018, the adult female gave birth to an unsexed infant, however, as young siamang do not leave their mother's side until they are three months or older, its behaviour was not considered in this study. Christopher Marsh and Ucok Sahrizal habituated all siamang across both groups to human presence prior to this study. Hankinson (2017) estimated siamang populations densities to be between 0.40 – 2.11 groups/km^2 within the extended Sikundur area, although five to six groups were regularly heard calling within a c1.5km radius from camp.

3.3 Data collection

3.3.1 Vegetation assessment of sleeping trees and emergent non-sleeping trees

Siamang were followed from sleeping tree to subsequent sleeping tree (see section 3.3.2). Once siamang had slept in a tree, its location was marked with the GPS unit. On days when siamang follows were not scheduled, we returned to assess vegetation characteristics of sleeping trees and the surrounding background trees. Plots measuring 25x25m were established with the sleeping tree as the central point. Borders of the plots were oriented in a north-south and east-west direction. Sleeping trees were measured for the following variables: diameter at breast height (DBH), tree height, height to first major bole, crown width in a north, south, east, and west orientation, percentage estimate of canopy connected to the canopy of adjacent trees (canopy connectivity), percentage estimate of tree cover by vines and lianas, total number of branches 10-20cm in circumference and total number of branches over 20cm in circumference. From these measurements it was possible to calculate additional variables (Table 3.1). The same measurements were made on every tree with a DBH ≥10cm within the 25x25m plot.

Table 3.1 Variables collected from each vegetation plot.

Variable	Units	Explanation	Method
Diameter at breast height (DBH)	*cm*	Diameter of the trunk at approx. 1.3m from the ground.	Measure the tree trunk with a tape measure to calculate circumference at breast height and divide value by π.
Tree height	*m*	Top height of the tree from the ground up.	Use range finder.
Bole height	*m*	Height from the ground to the first major separation of branches from the tree trunk of the tree.	Use range finder.
Height:DBH ratio	-	Tree height divided by DBH to give an indication of tree growth.	Tree height divided by DBH.
Crown area	m^2	Estimate of the crown area using measurements from the crown width, calculated by distance from the trunk of the tree to the north, south, east and west ordinal points of the crown	Using a tape measure, pace out the distance from the trunk to the furthest point of the crown, then use the following equation: Crown area = $\pi\ (\frac{N+Swidth}{2})\ \text{x}\ (\frac{E+Wwidth}{2})$
Crown height	*m*	Height from the first major bole to the top height of the tree.	Top height minus bole height.
Canopy connectivity	*%*	Percentage estimate of crown of focal tree connected to the crown of adjacent trees.	Looking at the crown of the tree as a whole, estimate the percentage of canopy connectivity 0-100%.
Vines and lianas	*%*	Percentage estimate of whole tree covered in vines and lianas.	Looking at the whole tree, estimate the percentage of coverage 0-100%.
No. branches 10-20cm	*#*	Count of all branches on focal tree between 10-20cm in circumference.	Count all branches with a circumference of 10-20cm.
No. branches >20cm	*#*	Count of all branches on focal tree over 20cm in circumference.	Count all branches with a circumference of 20cm or more.
Tree density	*trees per hectare*	Number of trees per plot with DBH ≥10cm, per hectare.	Number of trees in each plot with DBH ≥10cm, multiplied by 16.

Terminology for the different tree types is show in Table 3.2. Heights were measured with a Nikon Forestry Pro Laser Rangefinder. As a correction factor, all tree heights that were measured with the range finder were multiplied by tree opposed to which vegetation characteristics do not, 22 tall, emergent trees were identified that were not used by siamang as sleeping trees during the period of this study. The same vegetation measures were recorded for these emergent non-sleeping trees as for the sleeping trees.

Nineteen of these trees were identified using Unmanned Aerial Vehicle (UAV) data obtained from Alexander *et al*. (2018), with an additional three selected by visual means along the manmade trails within the monitoring system. All emergent non-sleeping tree plots assessed were within the area which both siamang groups occupied. Both sleeping trees and emergent, non-sleeping trees were identified to local species names and then later described into their respective families.

Table 3.2 Terminologies and explanations of the different tree types within vegetation plots.

Term	Explanation
Emergent trees	Trees with part of the trunk and the crown exposed above the surrounding mean canopy height.
Sleeping trees	Emergent trees used by siamang during the period of this study.
Non-sleeping trees	Emergent trees not used by siamang during the period of this study.
Centralised trees	Emergent trees, either sleeping or non-sleeping, that form the centre point of a 25x25m vegetation plot.
Background tree	All other trees within a 25x25m vegetation plot that are not the centralised tree with a DBH >10cm.

3.3.2 Siamang follows

Follows began on Group A on 27th April 2018 and on Group B on 23rd May 2018. Siamang groups were followed for 3-5 consecutive days, from sleeping tree (if known) to subsequent sleeping tree. If the previous night's sleeping tree was not known, siamang were located by searching in areas where they are known to frequent within their home ranges or by following their morning long calls. Group A was followed for a total of 27 days, consisting of 22 complete day follows and five incomplete day follows,

and Group B was followed for a total of 26 days, consisting of 12 complete days and 14 incomplete days. Complete day follows were when siamang were followed from sleeping tree to sleeping tree, and incomplete day follows were when the previous night's sleeping tree was unknown, or if observers lost track of the group due to unfavourable terrain/vegetation, or if the follow was abandoned in adverse weather conditions. Breakdowns of follows across both groups are show in Table 3.3. Complete day follows were far less successful for Group B due to her more elusive, solitary nature and because of the difficult landscapes she occupied. Once siamang were located, they were followed until they entered their sleeping trees between 15:00 and 19:00 hr. On days when Group A was followed, the observers would visit the known sleeping trees of Group B in the evening and vice versa to get a greater sample of frequency of tree use. This method also identified whether other species or other groups of hylobatid were using the same trees when the focal groups were not there. Successful evening visits were made to Group A sleeping trees 33 times and to Group B sleeping trees 14 times.

Table 3.3 Breakdown of siamang follows.

	Complete day follows		**Incomplete day follows**		**Total**	
Group	**No. of days**	**Average time**	**No. of days**	**Average time**	**No. of days**	**Time followed**
A	22	11 hrs 14 mins	5	6 hrs 54 mins	27	281 hrs 42 mins
B	12	10 hrs 11 mins	14	6 hrs 12 mins	26	209 hrs 07 mins

During siamang follows, behavioural data were documented using the five-minute scan sampling technique, recorded using the Animal Observer application (v1.0) on an Apple iPad (Caillaud, 2016). The advantage of using a tablet to record behavioural data is that it's possible to instantaneously record the behaviour of multiple individuals with a few

taps and the data downloads in a comma separated file (.csv) format ready for analysis. The behaviours of each individual were recorded every five minutes (Table 3.4), including estimated heights of each individual in a tree, as well as the estimated tree height, and the distance between each individual (Group A only). GPS locations were recorded every 30 minutes using a Garmin GPSMAP 64S to establish home ranges and travel paths, and this information was linked to the behavioural scans of the siamang. Each long call location was marked using the GPS unit, independent of the five-minute scan samples and 30-minute GPS recordings, as well as duration of each call, and frequency of calls per day.

Table 3.4 Behaviours recorded using five-minute scan sampling.

Behaviours		
Level 1	**Level 2**	**Level 3**
Feeding	Leaves	Young leaves
		Stem
	Fruit	Whole fruit
		Seed
		Juice
		Skin
		Flesh
	Other	Insect
		Drinking
		Other
Travel *Includes brachiation, bipedal walking, climbing and jumping*	-	-
Resting *Includes laying, leaning, sleeping, hanging and sitting*	-	-
Socialising	Grooming	-
	Playing/fighting	-
	Inter-group interaction	-
	Long call	-

3.3.3 Sleeping behaviours

The time individual siamang entered a sleeping tree and the time they reached their final sleeping position were recorded. When siamang entered a new sleeping tree we waited for ≥30 minutes to make sure that was in fact a sleeping tree and that the siamang were sleeping. Sleeping location on a sleeping tree was categorised into: close to trunk, middle of branch, and end of branch (Fig. 3.3). The height of each sleeping individual was also recorded, as well as the height of the tree and the height of the first major bole using the rangefinder. The distance between individuals of Group A was measured by standing underneath their sleeping position and recording with a tape measure. In the mornings, siamang typically began to move within their sleeping tree before there was enough light for visibility, so the time they were first heard moving was noted. These movements were usually the sound of branch and leaf movement or by short vocalisations between the two males squabbling. The time each individual left the sleeping tree was also noted as well as if they had moved sleeping trees during the night.

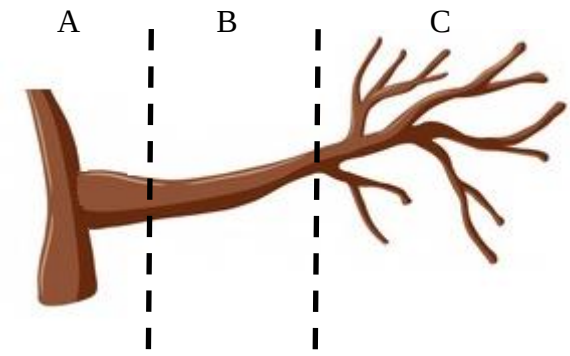


Figure 3.3 Possible siamang sleeping locations on a branch. Area A = ‘close to trunk’; area B = ‘middle of branch’; area C = ‘end of branch’.

3.4 Data analyses

Data were assessed for normality before any statistical comparison took place, using the Shapiro-Wilk test. As most of the vegetation variables were not normally distributed, non-parametric statistical analysis (Mann-Whitney *U*) were applied to identify any significant differences between sleeping trees and emergent non-sleeping trees, as well as between the background trees of the two different plot types (sleeping against non-sleeping). A generalised linear model (GLM) was also created to select for the strongest predictive models to support the Mann-Whitney *U* results. To account for differences between solitary and group living, sleeping trees and background trees in sleeping plots were also compared between Group A and Group B using Mann-Whitney *U*. The expected and observed frequencies of sleeping tree use were compared using chi-squared goodness of fit test (X^2; Siegel & Castellan, 1988). To understand if siamang preferred sleeping trees closer to fruiting trees, the time taken from sleeping trees to reach the first fruiting tree and from last fruiting tree to sleeping tree were calculated from the five-minute behaviour scan samples. These scan samples were also used to determine whether siamang selected sleeping trees based on comfort by calculating the number of rests per day. Distance to fruiting trees and number of rests were both analysed using non-parametric Kruskal-Wallis tests, but were only considered for Group A as the re-use rate and sample size of sleeping trees of Group B were not large enough for statistical consideration. Log_{10} transformations were considered on data that were not distributed normally, but this also returned data with non-normal distributions, and was therefore not applied. All *p*-values were two-tailed, with the alpha level set to 0.05. Sequential Bonferroni corrections were applied to all Mann-Whitney *U* tests and the alternative *p* is indicated where necessary. When considering siamang movements in and out of sleeping trees, time was expressed in minutes in relation to sunrise and sunset

to avoid seasonal and daylight bias (obtained from the GPS unit in the field). Where applicable, plus minus (±) represents one standard deviation. All data were managed in Microsoft Excel (v.14.7.7) with statistical analyses carried out in RStudio (v.1.1.456) and spatial data processed in ArcMap (v.10.1).

3.5 Ethical note

The necessary local and national authorities including the Ministry of Research, Technology and Higher Education of the Republic of Indonesia (RISTEKDIKTI), Conservation of Natural Resource, Indonesia (BKSDA), and Taman Nasional Gunung Leuser (TNGL) approved the research reported in this thesis. All research activities adhered to the ethical recommendations outlined by the Association for the Study of Animal Behaviour (ASAB), in accordance with the Primate Society of Great Britain (PSBG).

4. RESULTS

4.1 Vegetation analysis

A total of 43 vegetation plots were assessed (sleeping tree plots n = 21, non-sleeping tree plots n = 22) across the range of the two siamang groups. A total of 467 individual trees were measured with 43 trees being the emergent, centralised tree and 424 trees being classified as background trees within the plots. As the sample size for background trees was considerably larger than the sample size for sleeping and non-sleeping trees, the median values of each plot variable were used for Mann-Whitney U statistical analysis unless otherwise stated. This way, plots are independent from one another, but trees within plots have similar statistical value.

4.1.1 Differences between sleeping trees and emergent non-sleeping trees

Sleeping trees have significantly higher canopy connectivity values (*Mdn* = 12%) than emergent non-sleeping trees (*Mdn* = 2.5%) (U = 86, p < 0.001; Fig. 4.1). Emergent non-sleeping trees had significantly more branches over 20cm in circumference (*Mdn* = 21) than sleeping trees did (*Mdn* = 9) (U = 379, p < 0.001; Fig. 4.2). There were no significant differences between siamang sleeping trees and emergent non-sleeping trees for DBH, tree height, bole height, height:DBH ratio, crown area, crown height, vines and lianas, and branches between 10-20cm in circumference (Table 4.1; Figs. 4.3 - 4.10).

4.1.2 Differences between background trees in sleeping plots and background trees in non-sleeping plots

Background trees in sleeping plots were significantly taller, had higher first major boles, and taller crown heights than background trees in non-sleeping plots (Table 4.1; Fig. 4.4; Fig. 4.5; Fig. 4.8). There was no significant difference between background trees in sleeping plots and background trees in non-sleeping plots for canopy connectivity, number of branches over 20cm in circumference, DBH, height:DBH ratio, crown area, vines and lianas, number of branches between 10-20cm in circumference, and tree density (Table 4.1; Figs.4.1 – 4.3; 4.6; 4.7; 4.9 – 4.11).

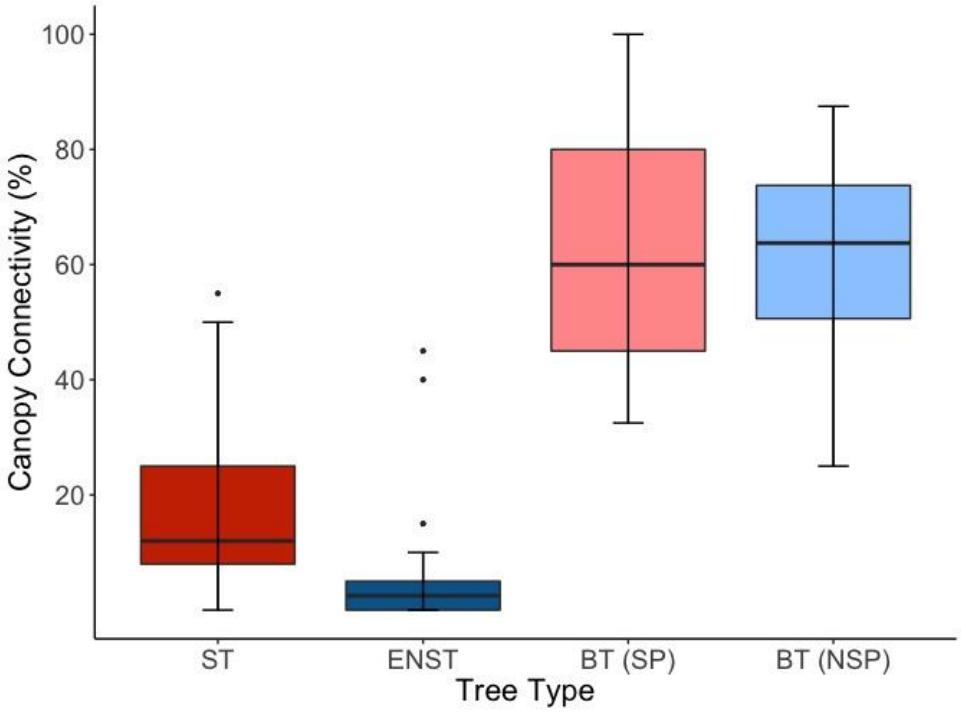


Figure 4.1 Canopy connectivity for the four tree groups (ST = sleeping trees, ENST = emergent non-sleeping trees, BT (SP) = background trees in sleeping plots, BT (NSP) = background trees in non-sleeping plots). Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

Table 4.1 Comparing sleeping trees with emergent non-sleeping trees and background trees in sleeping plots with background trees in non-sleeping plots. Significant *p*-values are shown in bold. *p*-values with * were not significant with sequential Bonferonni corrections.

Variable	Comparing siamang sleeping trees (ST) with emergent non-sleeping trees (ENST)						Comparing background trees in sleeping tree plots (SP) with background trees in non-sleeping tree plots (NSTP)					
	Group	***n***	**Median**	**IQR**	**U**	***p*-value**	**Group**	***n***	**Median**	**IQR**	**U**	***p*-value**
DBH (cm)	ST	21	111.46	59.87	301.5	0.089	SP	21	22.29	15.92	200	0.458
	ENST	22	133.6	81.21			NSP	22	21.97	4.54		
Tree Height (m)	ST	21	41.2	12.7	209	0.605	SP	21	15.5	5	144	**0.035***
	ENST	22	39.95	9.45			NSP	22	13.2	2.94		
Bole Height (m)	ST	21	30.9	9.53	271	0.341	SP	21	12.9	2.4	132	**0.016***
	ENST	22	29.96	7.09			NSP	22	10.14	1.87		
Height:DBH Ratio	ST	21	36.98	14.46	162	0.096	SP	21	59.91	17	194	0.379
	ENST	22	30.08	16.28			NSP	22	57.73	17.57		
Crown Area (m^2)	ST	21	227.42	218.88	225	0.895	SP	21	29.26	37.87	170	0.143
	ENST	22	224.97	134.24			NSP	22	23.92	17.3		
Crown Height (m)	ST	21	17.6	11.9	180	0.222	SP	21	6.4	2.65	148	**0.044***
	ENST	22	16.15	12.85			NSP	22	4.9	2.09		
Canopy Connectivity (%)	ST	21	12	17	86	**<0.001**	SP	21	60	35	225.5	0.903
	ENST	22	2.5	5			NSP	22	63.75	23.13		
Vines and Lianas (%)	ST	21	0	5	263	0.377	SP	21	0	5	248	0.657
	ENST	22	0	26.25			NSP	22	0	5		
No. Branches 10-20cm	ST	21	24	17	291	0.148	SP	21	2	1	170	0.129
	ENST	22	28.5	20.5			NSP	22	1	2		
No. Branches >20cm	ST	21	9	7	379	**<0.001**	SP	204**	0	0	22540	0.912
	ENST	22	21	18.75			NSP	220**	0	0		
Tree Density (per hectare) †	ST	-	-	-	-	-	SP	21	176	96	232	0.99
	ENST	-	-	-			NSP	22	176	64		

†Tree Density includes central sleeping trees and emergent non-sleeping trees. **All trees were considered instead of medians per plot for this variable as plot medians were skewed towards zero.

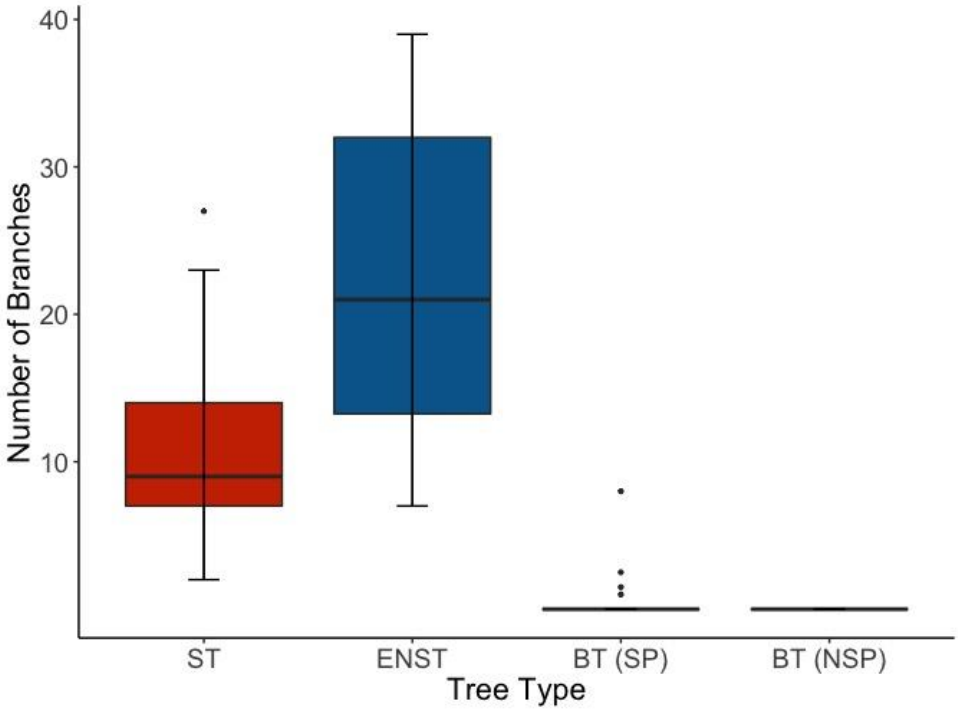


Figure 4.2 Number of branches over 20cm in circumference for the four tree groups (ST = sleeping trees, ENST = emergent non-sleeping trees, BT (SP) = background trees in sleeping plots, BT (NSP) = backgrounds tree non-sleeping plots). Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

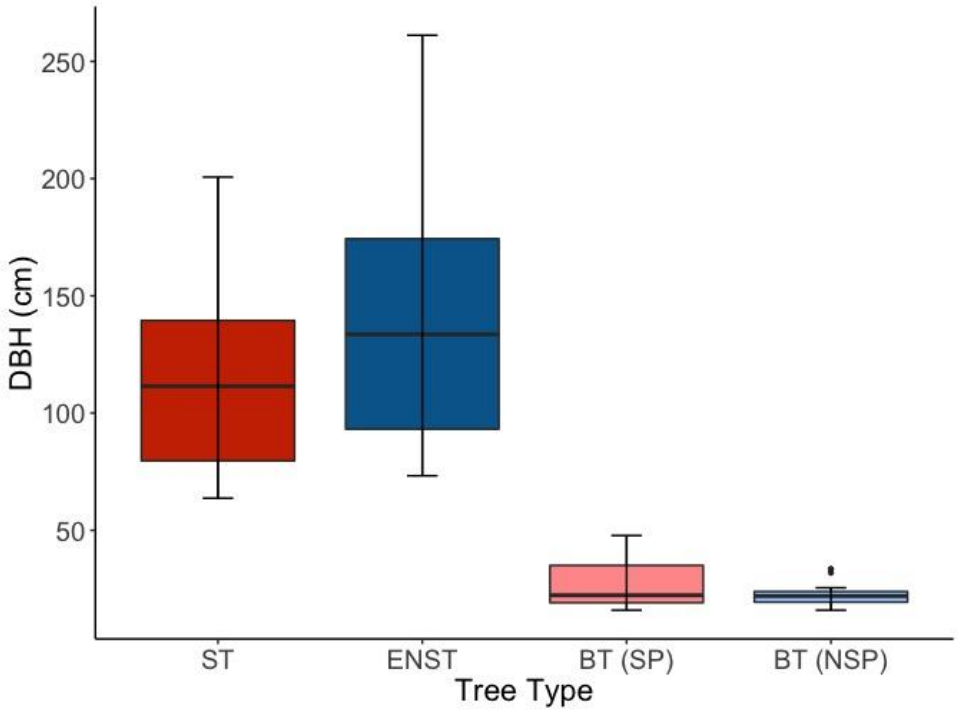


Figure 4.3 Diameter at breast height (DBH) for the four tree groups (ST = sleeping trees, ENST = emergent non-sleeping trees, BT (SP) = background trees in sleeping plots, BT (NSP) = background trees in non-sleeping plots). Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

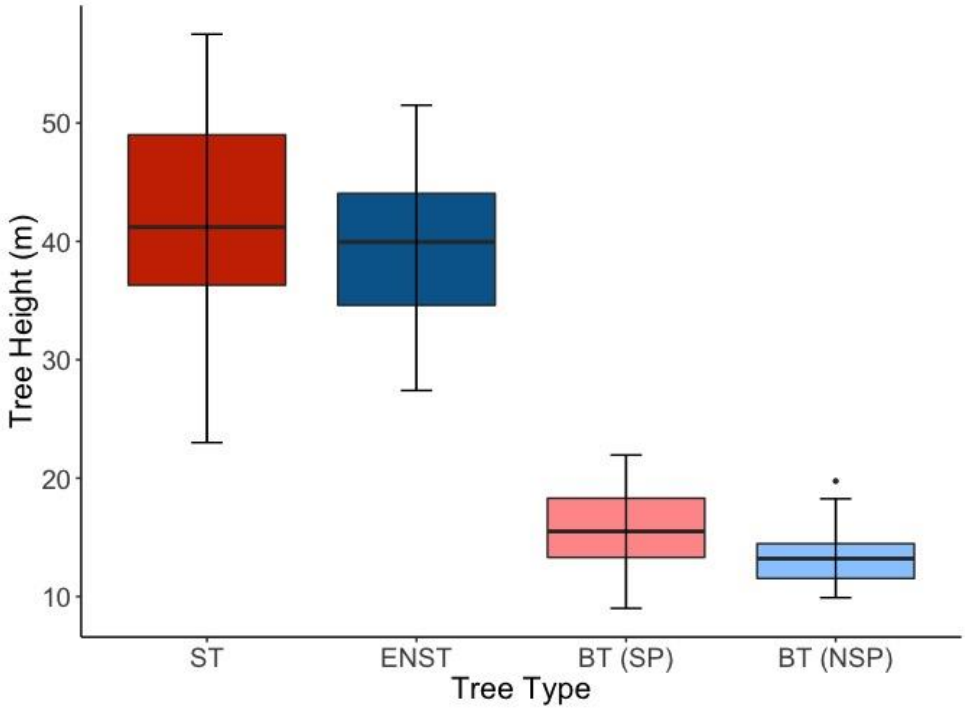


Figure 4.4 Tree height for the four tree groups (ST = sleeping trees, ENST = emergent non-sleeping trees, BT (SP) = background trees in sleeping plots, BT (NSP) = background trees in non-sleeping plots). Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

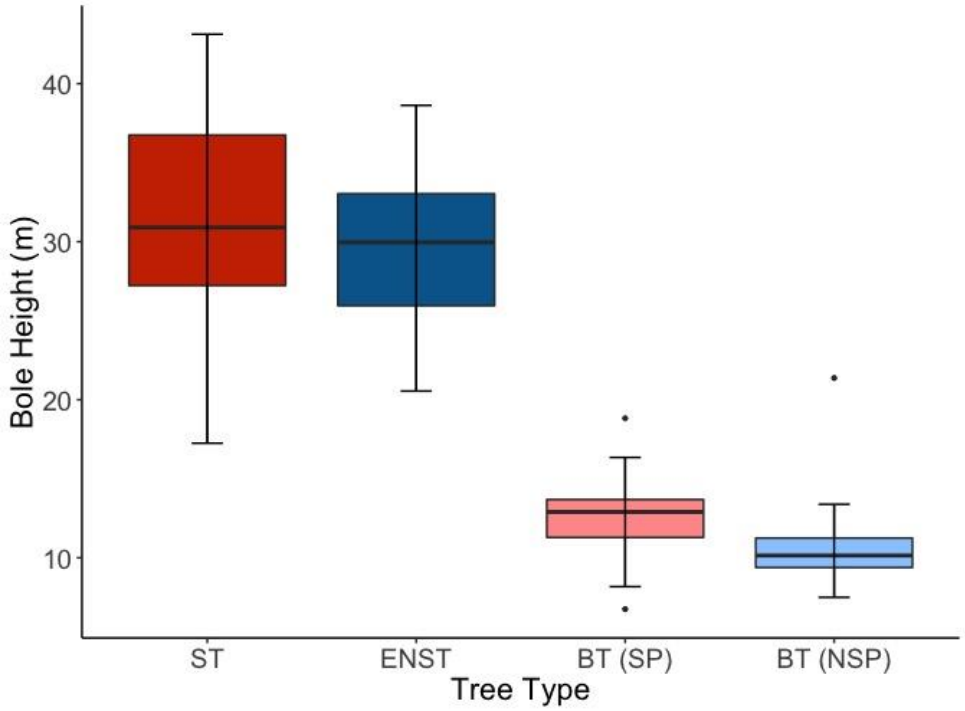


Figure 4.5 Height to first major bole for the four tree groups (ST = sleeping trees, ENST = emergent non-sleeping trees, BT (SP) = background trees in sleeping plots, BT (NSP) = background trees in non-sleeping plots). Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

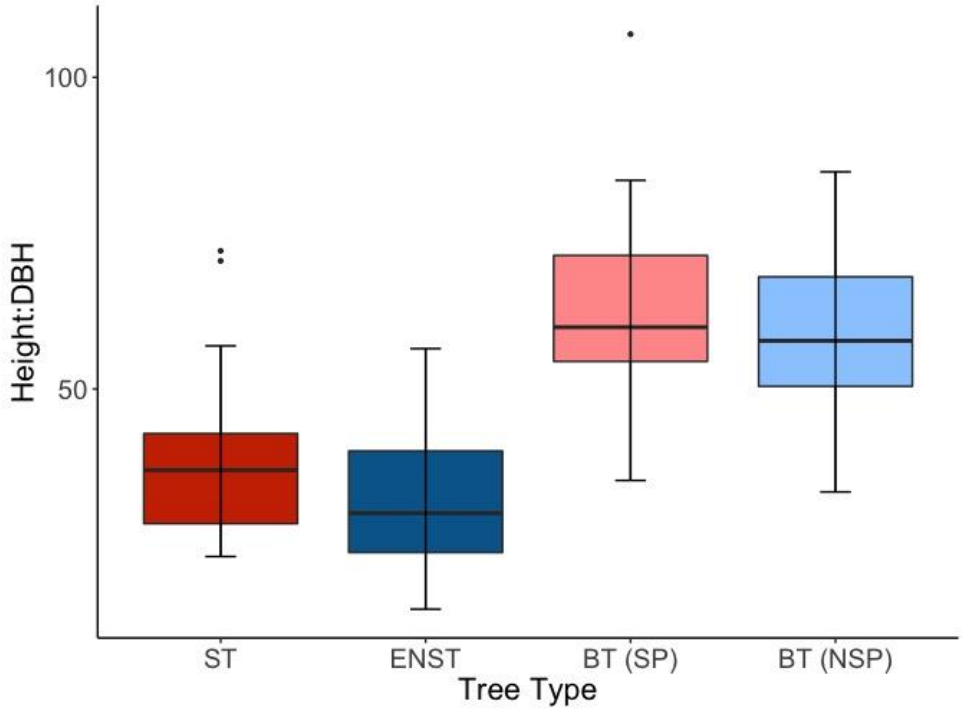


Figure 4.6 Height:DBH ratio for the four tree groups (ST = sleeping trees, ENST = emergent non-sleeping trees, BT (SP) = background trees in sleeping plots, BT (NSP) = background trees in non-sleeping plots). Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

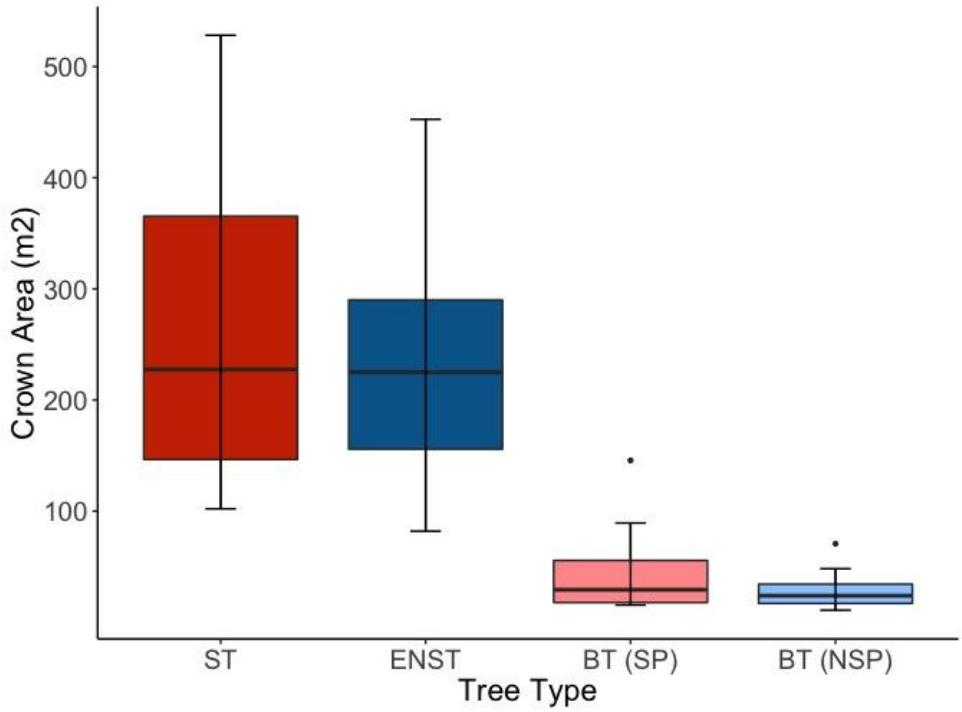


Figure 4.7 Crown area for the four tree groups (ST = sleeping trees, ENST = emergent non-sleeping trees, BT (SP) = background trees in sleeping plots, BT (NSP) = background trees in non-sleeping plots). Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

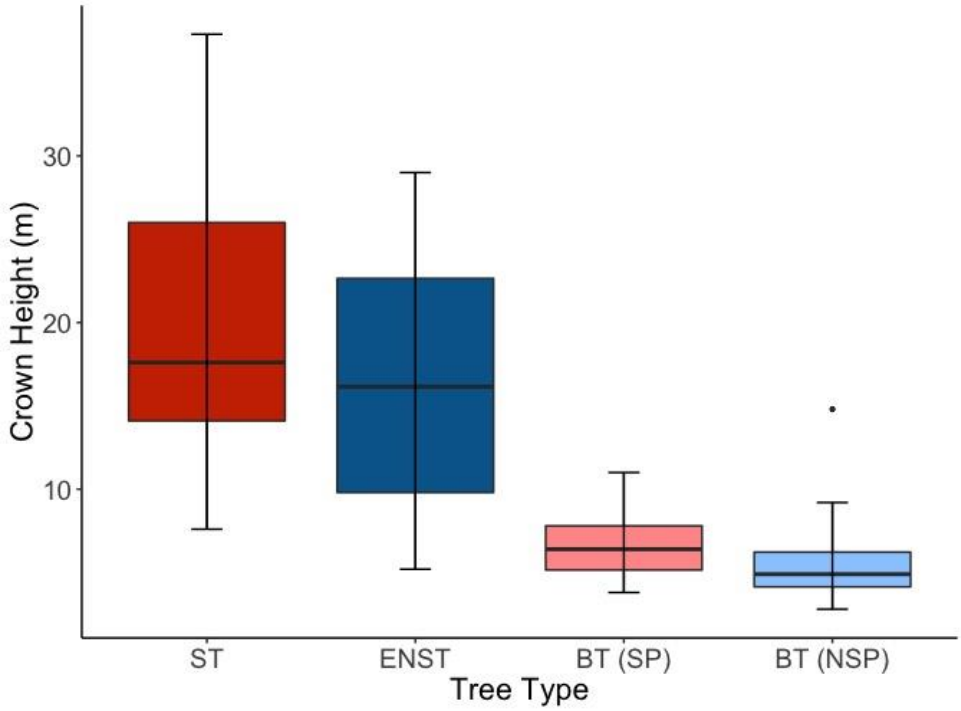


Figure 4.8 Crown height for the four tree groups (ST = sleeping trees, ENST = emergent non-sleeping trees, BT (SP) = background trees in sleeping plots, BT (NSP) = background trees in non-sleeping plots). Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

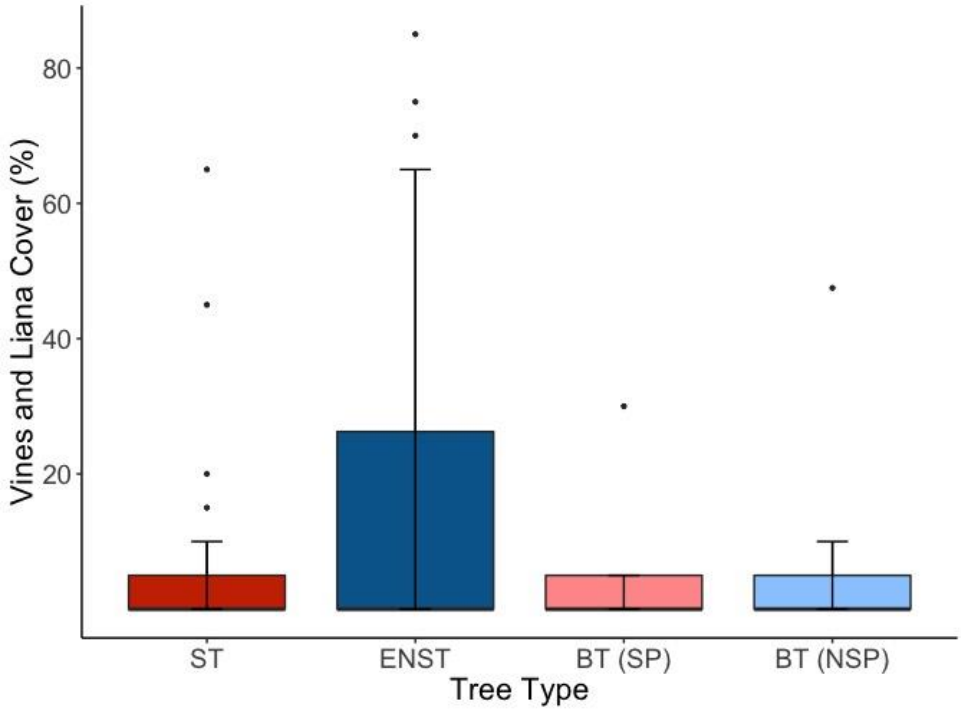


Figure 4.9 Vines and liana cover for the four tree groups (ST = sleeping trees, ENST = emergent non-sleeping trees, BT (SP) = background trees in sleeping plots, BT (NSP) = background trees in non-sleeping plots). Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

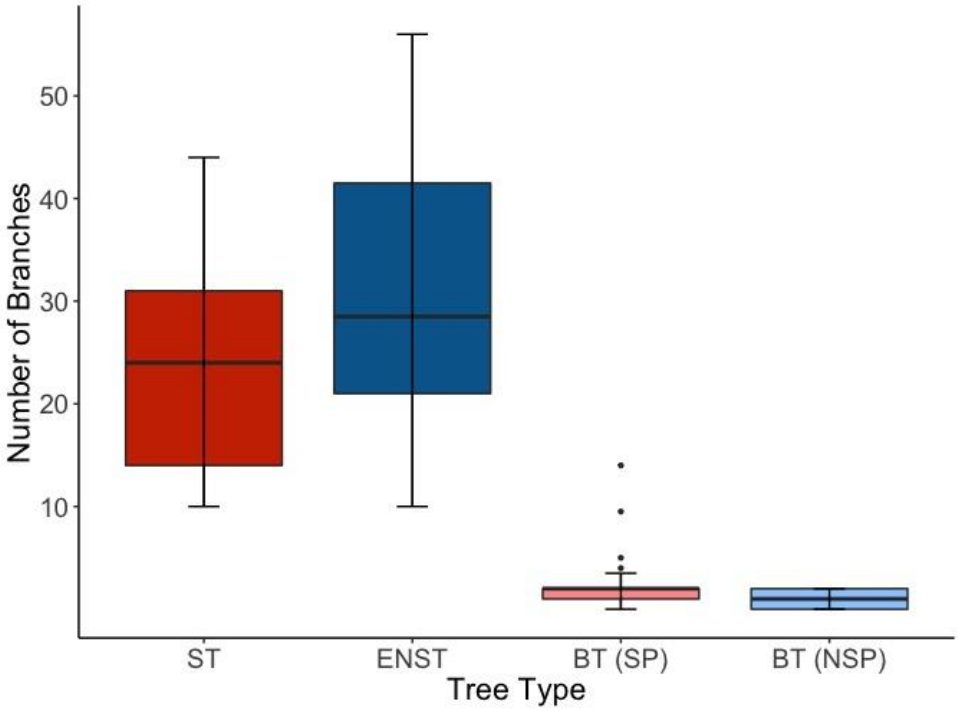


Figure 4.10 Number of branches between 10-20cm in circumference for the four tree groups (ST = sleeping trees, ENST = emergent non-sleeping trees, BT (SP) = background trees in sleeping plots, BT (NSP) = backgrounds tree non-sleeping plots). Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

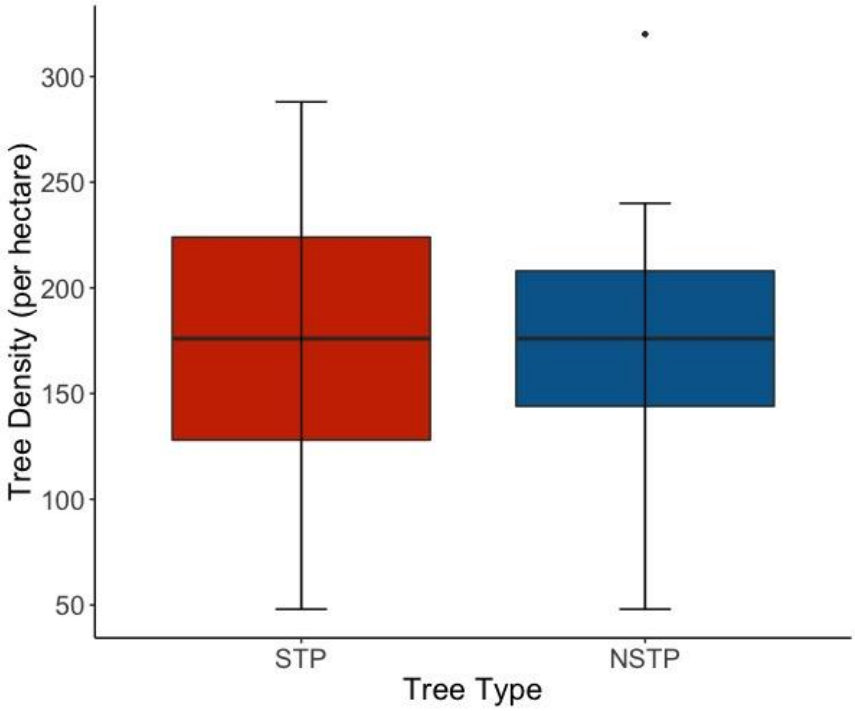


Figure 4.11 Tree density for the two plot types (STP = sleeping tree plot, NSTP = non-sleeping tree plot. Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

4.1.3 Vegetation analysis (through a generalised linear model)

To support the findings of Mann-Whitney *U* tests on differences between sleeping trees and emergent non-sleeping trees, as well as the differences between background trees in sleeping plots and background trees in non-sleeping plots, vegetation data were assessed through a generalised linear model (GLM). First, all vegetation variables were considered in a fully parameterised GLM for sleeping trees against emergent non-sleeping trees (Table 4.2), and for background trees in sleeping plots and background trees in non-sleeping plots (Table 4.3). Vegetation variables were then selected for the strongest predictive models with the least number of predictor variables based on AICc values using the multi-model interface (MuMIn) package in R (Table 4.4; Bartoń, 2018). The value of AIC (Aikake's Information Criterion) indicates how well any given model fits observed variation within the data (Burnham & Anderson, 2002). Those variables that had equation values determined by the models, and that had a delta-AICc value of 2 or less were then considered for the final GLMs (Tables 4.5 - 4.6).

Table 4.2 Fully parameterised GLM comparing sleeping trees to emergent non-sleeping trees. Significant *p*-values (≤0.05) are highlighted in bold.

	Estimate	**Std. Error**	**z value**	**pr(>|z|)**
(Intercept)	-13.980	7.779	-1.797	0.072
DBH	0.129	0.056	2.195	**0.028**
Tree Height	-0.184	0.154	-1.190	0.234
Bole Height	0.147	0.091	1.615	0.106
Height:DBH ratio	0.110	0.116	0.943	0.346
Crown Area	-0.030	0.017	-1.806	0.071
Canopy Connectivity	0.088	0.070	1.266	0.205
Vines & Lianas	0.044	0.042	1.051	0.293
No. Branches 10-20cm	-0.153	0.123	-1.247	0.212
No. Branches >20cm	0.553	0.265	2.082	**0.037**

Crown Height was excluded from this model as values were retuned as NA.

Table 4.3 Fully parameterised GLM comparing median values of background trees in sleeping plots vs. median values of background trees in non-sleeping plots.

	Estimate	**Std. Error**	**z value**	**pr(>|z|)**
(Intercept)	7.004	4.819	1.453	0.146
DBH	0.132	0.202	0.654	0.513
Tree Height	-0.024	0.045	-0.888	0.600
Bole Height	-0.028	0.273	-0.102	0.919
Height:DBH ratio	-0.020	0.227	-0.888	0.374
Crown Height	-0.051	0.164	-0.309	0.757
Crown Area	-0.058	0.038	-1.529	0.126
Canopy Connectivity	-0.058	0.028	-0.207	0.836
Vines & Lianas	-0.193	0.058	-0.336	0.737
No. Branches 10-20cm	-0.046	0.460	-1.011	0.312
No. Branches >20cm	-15.53	1.800	-0.009	0.993
Tree Density	-0.009	0.009	-1.040	0.298

Table 4.4 See next page.

Table 4.5 Based on the best performing GLM (Table 4.4), the variables were included in the best fitting model for separating sleeping trees from emergent non-sleeping trees. Significant *p*-values (≤0.05) are highlighted in bold.

	Estimate	**Std. Error**	**z value**	**pr(>|z|)**
(Intercept)	-3.829	1.662	-2.298	**0.022**
Crown Height	-0.149	0.058	-2.547	**0.011**
DBH	0.031	0.011	2.700	**0.007**
No. Branches >20cm	0.222	0.073	3.031	**0.002***
Null deviance: 59.587 on 42 degrees of freedom				
Residual deviance: 30.540 on 39 degrees of freedom				
AIC: 38.54				

*Corresponds with Mann-Whitney *U* significance.

Table 4.6 Based on the best performing GLM (Table 4.4), the variables were included in the best fitting model for separating median values of background trees in sleeping plots vs. median values of background trees in non-sleeping plots.

	Estimate	**Std. Error**	**z value**	**pr(>|z|)**
(Intercept)	3.682	1.939	1.903	0.057
Bole Height	-0.142	0.111	-1.279	0.201
Height:DBH ratio	-0.020	0.019	-1.062	0.288
No. Branches >20cm	-16.195	1835.590	-0.009	0.993
Null deviance: 59.587 on 42 degrees of freedom				
Residual deviance: 43.427 on 31 degrees of freedom				
AIC: 67.427				

Table 4.4 GLM model results showing the best performing models with a delta AICc of <2 for sleeping trees versus emergent non-sleeping trees and background trees from sleeping tree plots versus background trees from non-sleeping tree plots based on a dredge performed using the MuMIn package (Bartoń, 2018) extracted from the fully parameterised model.

Model No.	*Intercept*	*Bole Height*	*No. Branches 10-20cm*	*No. Branches >20cm*	*Canopy Connectivity*	*Crown Area*	*Crown Height*	*DBH*	*Height:DBH Ratio*	*Tree Height*	*Vines & Lianas*	*Tree Density*	*df*	*logLik*	*AICc*	*delta*	*weight*
Sleeping trees vs. emergent non-sleeping trees																	
85	-6.807	-	-	0.281	-	-0.029	-	0.072	-	-	-		4	-13.960	37.0	0.00	0.048
117	-5.191	-	-	0.254	-	-0.020	-0.088	0.063	-	-	-		5	-12.756	37.1	0.16	0.044
119	-4.183	-	-0.102	0.364	-	-0.020	-0.111	0.059	-	-	-		6	-11.782	37.9	0.93	0.030
86	-8.926	0.078	-	0.268	-	-0.030	-	0.075	-	-	-		5	-13.188	38.0	1.03	0.029
597	-7.249	-	-	0.296	-	-0.030	-	0.074	-	-	0.032		5	-13.347	38.3	1.34	0.024
87	-5.910	-	-0.077	0.357	-	-0.025	-	0.066	-	-	-		5	-13.355	38.3	1.36	0.024
103	-3.152	-	-0.114	0.363	-	-	-0.168	0.036	-	-	-		5	-13.465	38.6	1.58	0.022
599	-6.551	-	-0.120	0.441	-	-0.027	-	0.069	-	-	0.046		6	-12.161	38.7	1.68	0.021
Background trees in sleeping plots vs. background trees in non-sleeping plots																	
147	6.044	-	-0.513	-	-	-0.042	-	-	-0.048	-	-	-	4	-23.451	56.0	0.00	0.014
659	8.484	-	-0.574	-	-	-0.057	-	-	-0.052	-	-	-0.088	5	-22.567	56.8	0.80	0.010
6	2.346	-0.169	-	-15.59	-	-	-	-	-	-	-	-	3	-25.182	57.0	1.02	0.009
149	4.684	-	-	-15.56	-	-0.036	-	-	-0.041	-	-	-	4	-24.133	57.3	1.36	0.007
145	5.267	-	-	-	-	-0.050	-	-	-0.045	-	-	-	3	-25.355	57.3	1.37	0.007
14	4.259	-0.199	-	-16.16	-0.024	-	-	-	-	-	-	-	4	-24.264	57.6	1.63	0.006
133	2.466	-	-	-16.90	-	-	-	-	-0.027	-	-	-	3	-25.482	57.6	1.63	0.006
518	4.569	-0.228	-	-16.07	-	-	-	-	-	-	-	-0.082	4	-24.297	57.6	1.69	0.006
5	0.258	-	-	-16.21	-	-	-	-	-		--	-	2	-26.711	57.7	1.77	0.006
12	5.267	-0.197	-0.547	-	-0.031	-	-	-	-	-	-	-	4	-24.367	57.8	1.83	0.006

4.1.4 Differences between sleeping sites used by the siamang group and the solitary female

Siamang living in a group slept in trees that had a significantly larger DBH, crown area and crown height, as well as those trees with significantly more branches 10-20cm in circumference, and those with a lower height:DBH ratio than a solitary individual (Table 4.7; Figs. 4.12 - 4.16). There was no significant difference between the two siamang groups for tree height, bole height, canopy connectivity, vines and lianas, and number of branches over 20cm in circumference for sleeping trees (Table 4.7). Background trees had a significantly lower height:DBH ratio in sleeping plots used by the group than the solitary female (Fig. 4.16), with the group also significantly favouring background trees with greater crown areas (Fig. 4.13; Table 4.7). There was no significant difference between background trees in sleeping plots used by Group A and those used by Group B for DBH, tree height, bole height, crown height, canopy connectivity, vines and lianas, number of branches between 10-20cm in circumference, number of branches over 20cm in circumference, and tree density (Table 4.7).

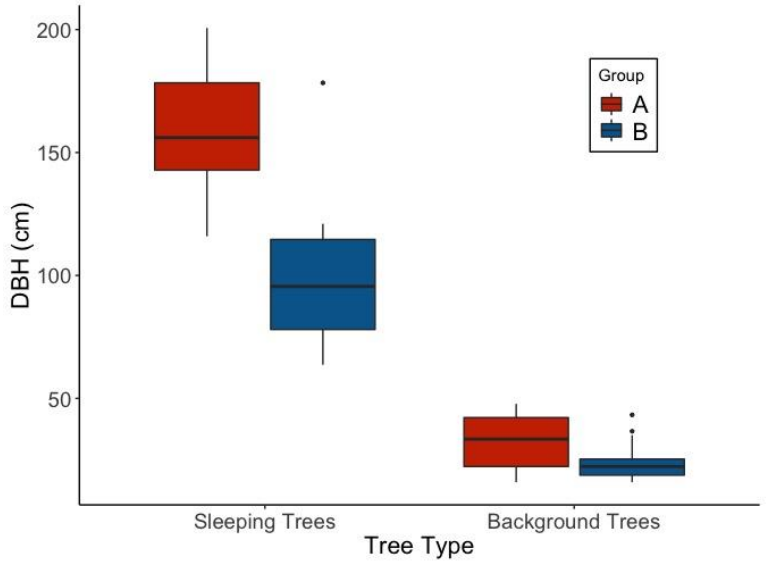


Figure 4.12 Diameter at breast height occupied by the two siamang groups. Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

Table 4.7 Comparing sleeping plots between siamang Group A and Group B. Significant *p*-values are shown in bold. *p*-values with * were not significant with sequential Bonferonni corrections.†Tree Density includes the central sleeping trees and emergent non-sleeping trees.

Variable	Comparing Group A sleeping trees with Group B sleeping trees						Comparing background trees in sleeping tree plots of Group A with background trees in sleeping tree plots of Group B					
	Group	***n***	**Median**	**IQR**	**U**	***p*-value**	**Group**	***n***	**Median**	**IQR**	**U**	***p*-value**
DBH (cm)	A	6	156.05	35.51	83	**0.003**	A	6	33.44	19.9	60.5	0.242
	B	15	95.54	36.62			B	15	22.29	6.53		
Tree Height (m)	A	6	46.75	13.7	61	0.235	A	6	15.05	3.01	33	0.381
	B	15	41.2	10.05			B	15	15.5	5.4		
Bole Height (m)	A	6	35.06	10.28	27	0.178	A	6	11.51	3.02	41	0.791
	B	15	30.9	7.74			B	15	13.2	3.02		
Height:DBH Ratio	A	6	27.95	7.86	17	**0.029***	A	6	41.62	13.56	11	**0.006***
	B	15	40.46	15.58			B	15	64.15	20.42		
Crown Area (m^2)	A	6	366.46	99.2	78	**0.008***	A	6	70.72	35.97	75	**0.018***
	B	15	177.81	101.55			B	15	20.6	15.72		
Crown Height (m)	A	6	29.05	10.78	75	**0.018***	A	6	6.45	1.6	41	0.791
	B	15	15.4	6.7			B	15	6	2.48		
Canopy Connectivity (%)	A	6	22.5	8.75	67.5	0.085	A	6	48.75	23.13	23	0.093
	B	15	10	11			B	15	70	40		
Vines and Lianas (%)	A	6	2.5	12.5	56	0.330	A	6	2.5	5	53.5	0.48
	B	15	0	2.5			B	15	0	5		
No. Branches 10-20cm	A	6	34.5	11	73.5	**0.029***	A	6	1.5	2.13	45	1
	B	15	17	12			B	15	2	1		
No. Branches >20cm	A	6	9	10.75	47.5	0.875	A	6	0	0.75	52	0.461
	B	15	9	6			B	15	0	0		
Tree Density (per hectare)†	-	-	-	-	-	-	A	6	152	112	40	0.725
	-	-	-	-			B	15	176	84		

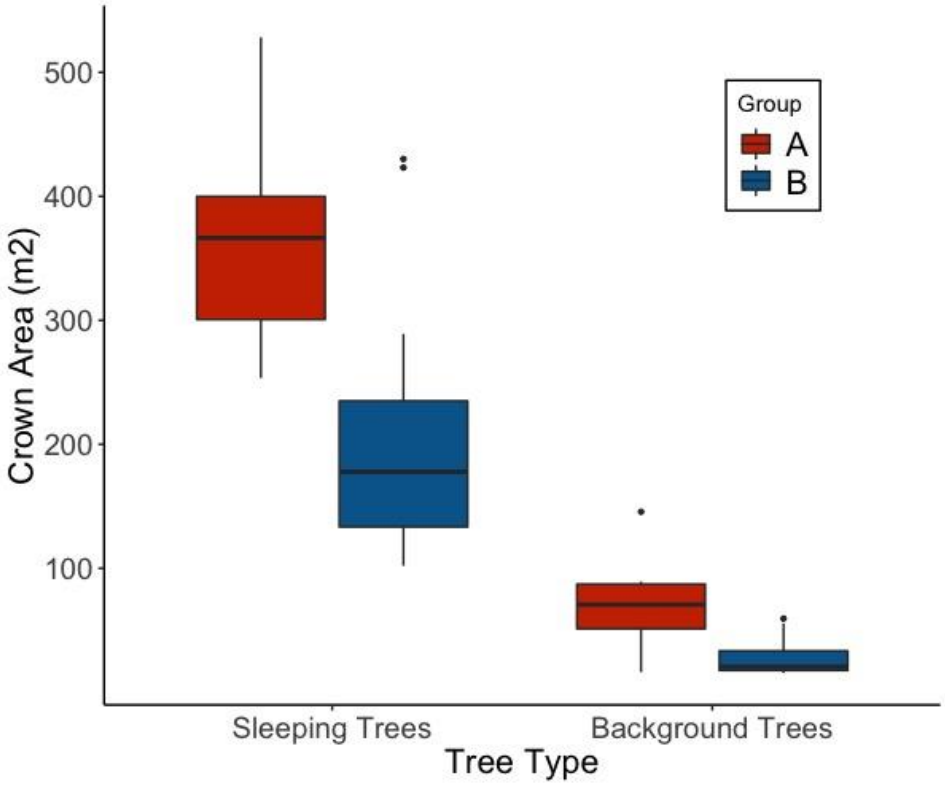


Figure 4.13 Crown area of trees occupied by the two siamang groups. Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

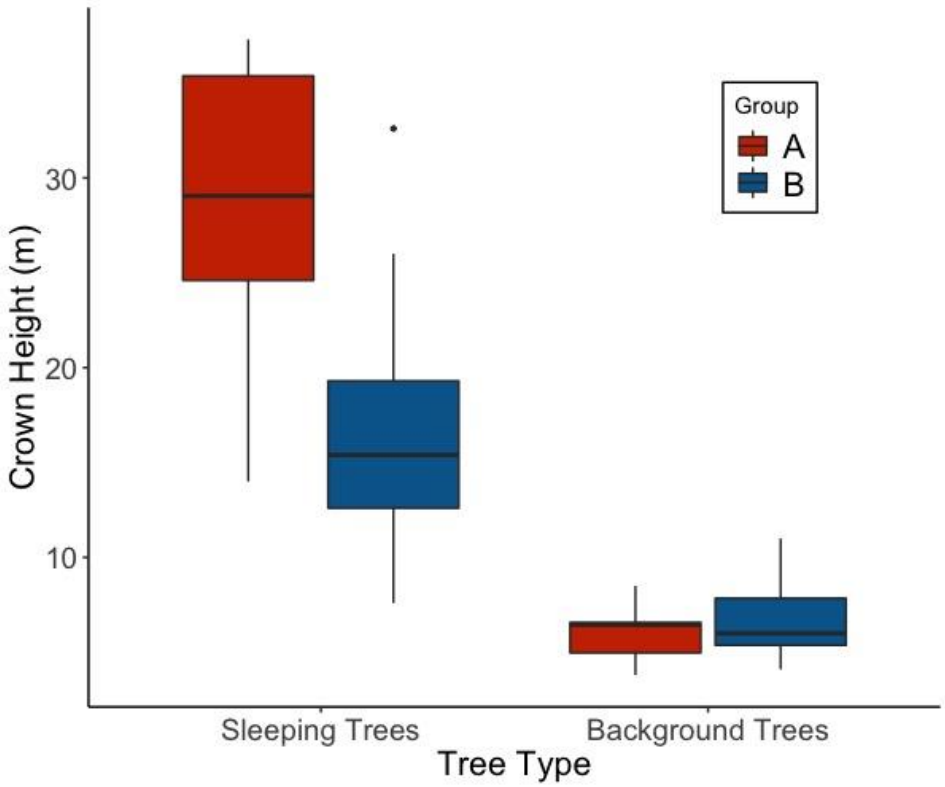


Figure 4.14 Crown height of trees occupied by the two siamang groups. Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

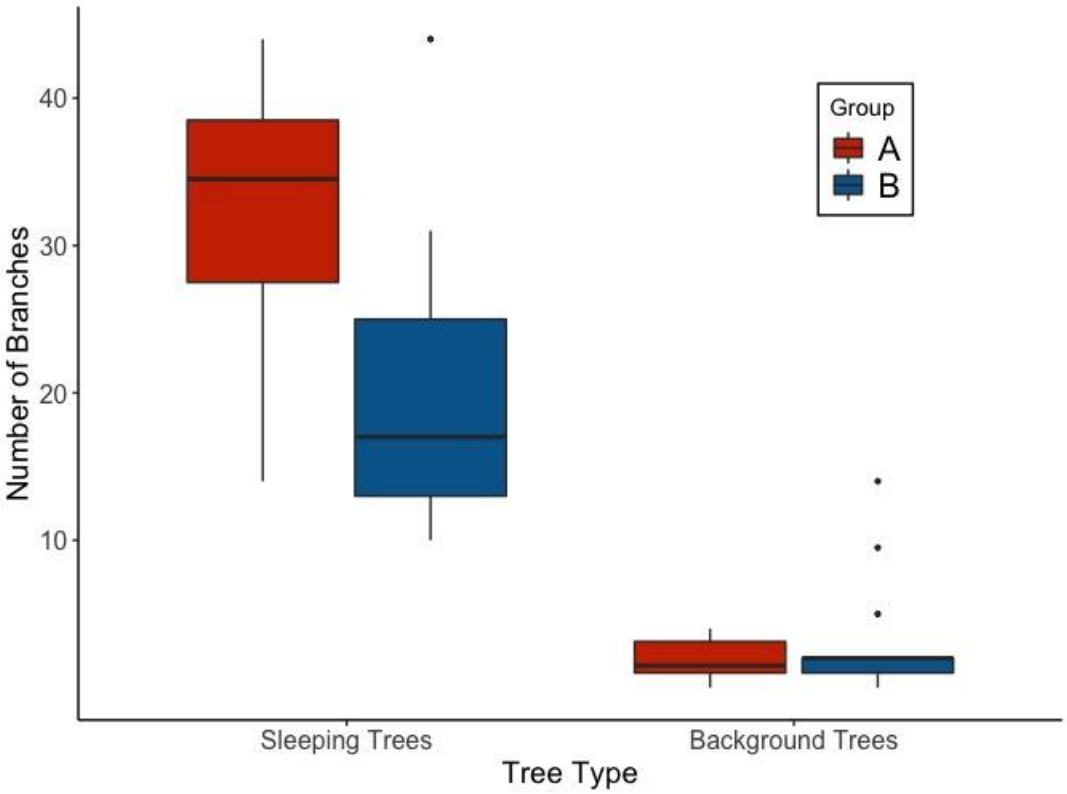


Figure 4.15 Number of branches between 10-20cm in circumference of trees occupied by the two siamang groups. Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

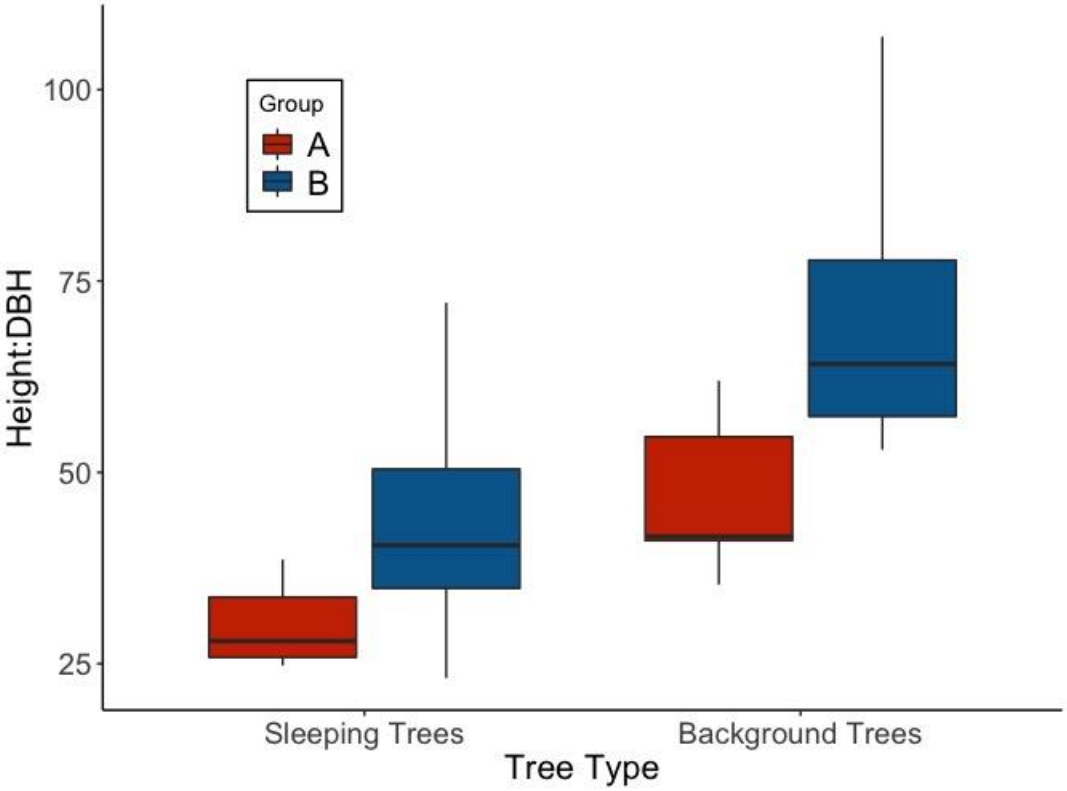


Figure 4.16 Height:DBH ratio of trees occupied by the two siamang groups. Boxes represent quartiles. Whiskers are set to 95th percentile. Dots represent outliers.

4.2 Sleeping tree use

During the study period, a total of 21 siamang sleeping trees were identified. Group A exclusively used four sleeping trees (60 observations), with an additional two identified by Christopher Marsh and Ucok Sahrizal (*pers. comm*. Dec 2017). These two additional trees were accounted for across all vegetation and spatial analysis, but were excluded elsewhere from the data, as direct observations of tree use during this study were not made. Group A re-used all of their sleeping trees on five or more occasions, with a significant difference between sleeping tree use (X^2 = 14.27, p = 0.003; Fig. 4.17). Group B used a total of 15 sleeping trees across 35 observations. Group B was less selective with sleeping trees, but there was also a significant difference between uses (X^2 = 126.28, p = 0.024; Fig. 4.18). As the sleeping location of both siamang groups was not recorded every night during the study period, the values displayed are the minimum of re-use for each sleeping tree.

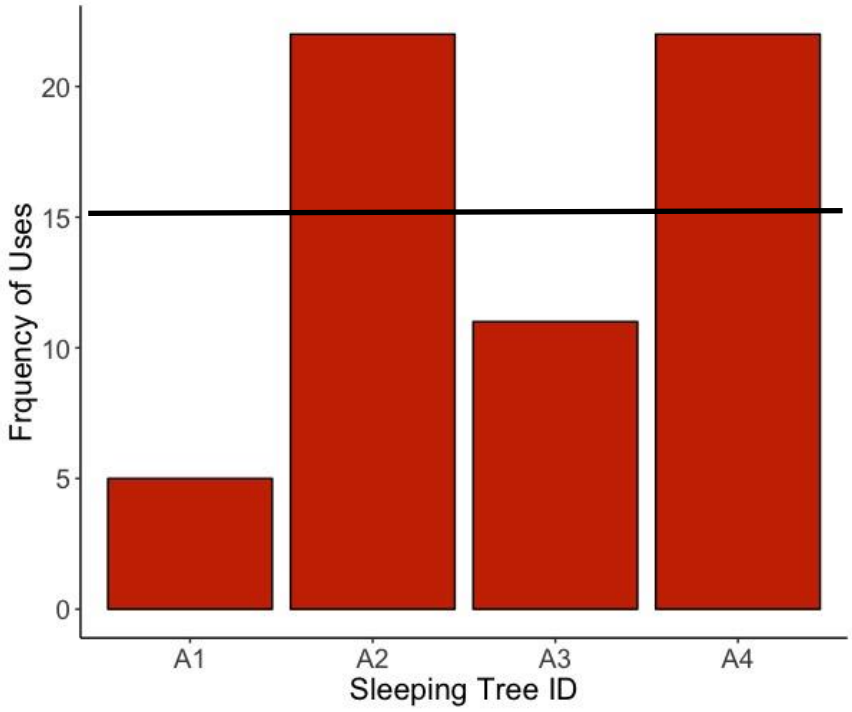


Figure 4.17 Frequency of use for each sleeping tree used by siamang Group A (n = 60 observations). The black line represents the expected values (n = 15 uses).

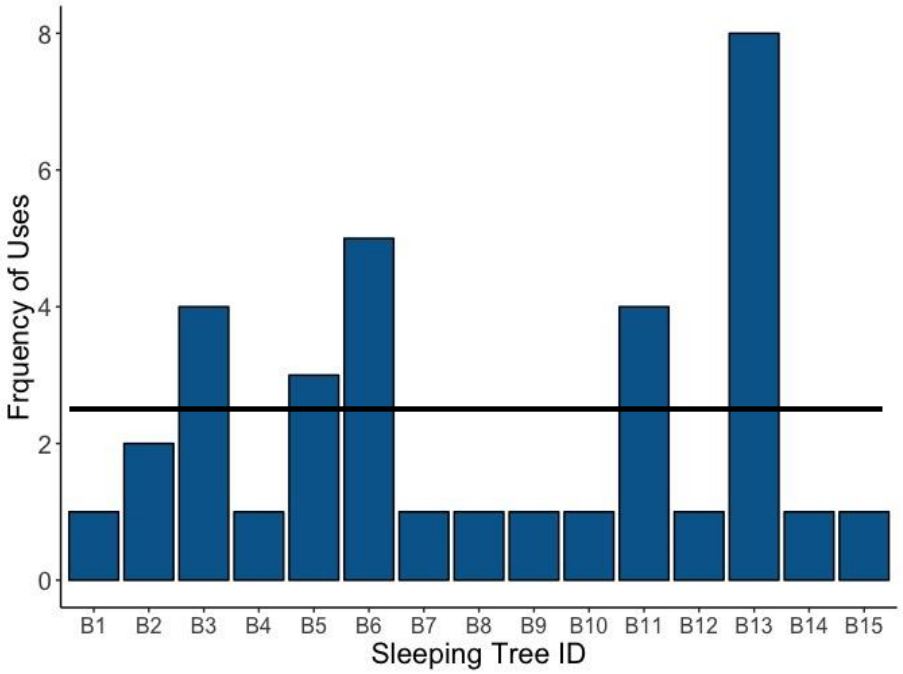


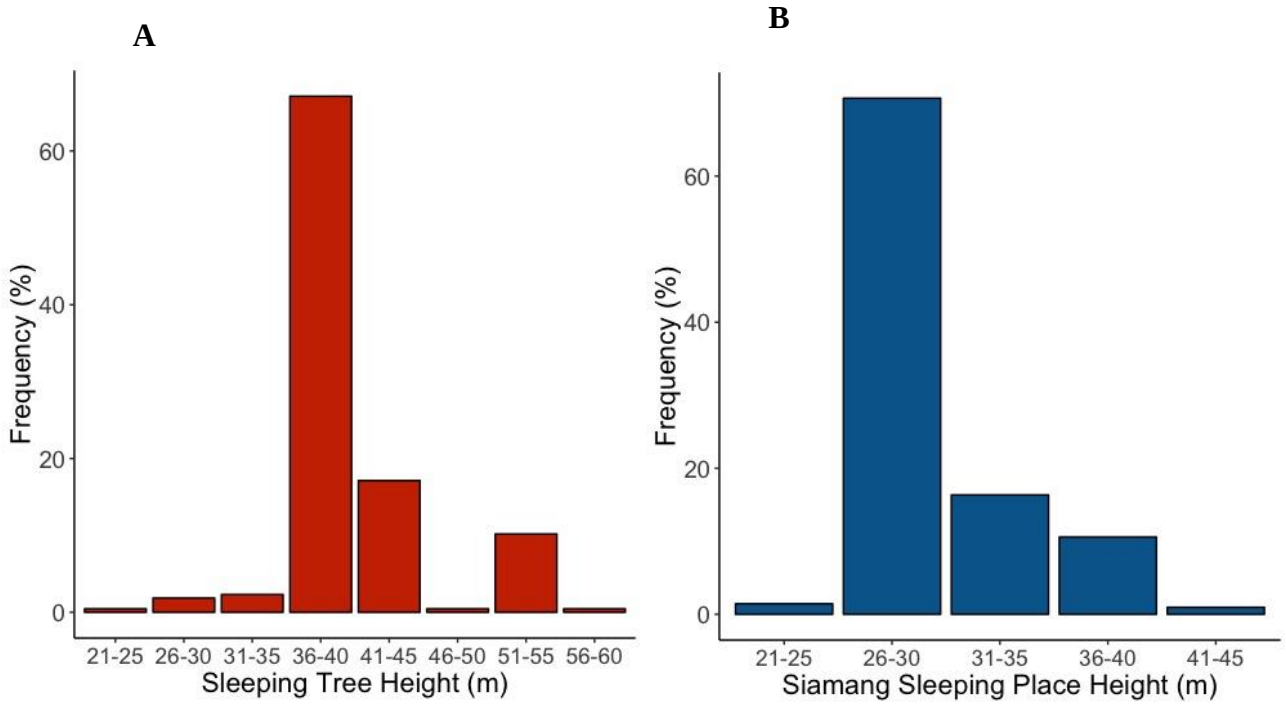
Figure 4.18 Frequency of use for each sleeping tree used by siamang Group B (*n* = 35 observation). The black line represents the expected values (*n* = 2.33 uses).

4.3 Sleeping behaviour

Members of Group A always slept in the same sleeping tree, with the adult male and sub-adult male often sleeping together in an embrace position or >1m apart (86%, *n* = 51) and the adult female on a separate branch. This is in accordance to other siamang studies where the males take an active role in caring for younger individuals (Lappan, 2008). Siamang entered sleeping trees 86 ± 60 minutes before sunset (*n* = 107) and reached their sleeping position within the sleeping tree 5 ± 20 minutes later (*n* = 99). Observers aimed to arrive approximately 30 minutes before sunrise, with the first siamang movements (branches moving, short vocalisations) were heard 25 ± 9 minutes before sunrise (*n* = 57), and siamang left the sleeping trees 15 ± 9 minutes later (*n* = 75). Siamang always entered sleeping trees before sunset (100%, *n* = 107) and generally (89%, *n* = 75) left sleeping trees before sunrise. Within the three sleeping position categories, siamang mostly slept at the end of branches (83%, *n* = 173 recorded sleeping

positions), occasionally at the middle point of a branch (15%, *n* = 32) and rarely near the trunk (2%, *n* = 4). Siamang slept 13.4 ± 6 metres from the top of the tree (*n* = 211), 7 ± 8.5 metres above the first major bole (*n* = 211), and 10.6 ± 3.9 metres above the mean canopy height (*n* = 210; Fig. 4.19).

Figure 4.19 Frequency distribution of sleeping tree heights (a) and siamang sleeping place height (b).



4.4 Distance to fruiting trees and sleeping tree comfort

Siamang did not chose sleeping trees based on the distance to fruiting trees. The distance (in time) from leaving the sleeping tree to arriving at the first fruiting tree did not differ significantly between the sleeping trees ($H = 0.77$, $p > 0.05$). There was also an insignificant difference between the distance (in time) from the last fruiting tree to the sleeping tree ($H = 5.04$, $p > 0.05$). There was however, a significant difference between the use of a sleeping tree and the number of rests per day from the five-minute scan samples ($H = 8.42$, $p = 0.02$), with Group A sleeping in tree A2 when they rested

throughout the day more frequently. This indicates siamang sleeping tree use is influences by tree comfort, as when they are more tired throughout the day they retire to a preferred sleeping site. There was, however, no significant difference between sleeping tree use and the number of rests the next day ($H = 3.41$, $p > 0.05$).

4.5 Home ranges and sleeping tree locations

A total of 1,015 GPS waypoints were collected across the two siamang groups from April to August (Group A, $n = 580$; Group B, $n = 436$). Kernel density estimates (KDE) for the two groups were calculated to identify areas of the forest most used by the siamang. Conventional KDE for primates are generally set to 50% for a core area and 95% for a peripheral area, however, there were no differences between core and periphery at these levels so the percentages were adjusted to 33%, 66% and 95% (Group A, Fig 4.20; Group B, Fig 4.21). Siamang did not have defined core areas as seen in other gibbon studies, and use the extremities of their home ranges at equal amounts as the central areas. Sleeping trees were located throughout home ranges and at the boundaries for both groups. A minimum convex polygon (MCP) was calculated for both groups with the arbitrary border representing the home range periphery. Group A's MCP home range was 7.5km^2 and Group B's MCP home range was 4.4km^2, with a clear overlap between Group A and Group B (Fig. 4.22). Group A had sleeping trees exclusively within their home range with the nearest one to Group B's home range approximately 205 metres away. Group B however had two sleeping trees in the overlap area with Group A. Emergent non-sleeping tree plots ($n = 22$) were distributed across both home ranges with 11 plots in Group A's home range, six plots in Group B's home range and five plots in the overlapping area (Fig. 4.22). Group A did not use the sleeping trees furthest north (A5) and south (A6) during the period of this study.

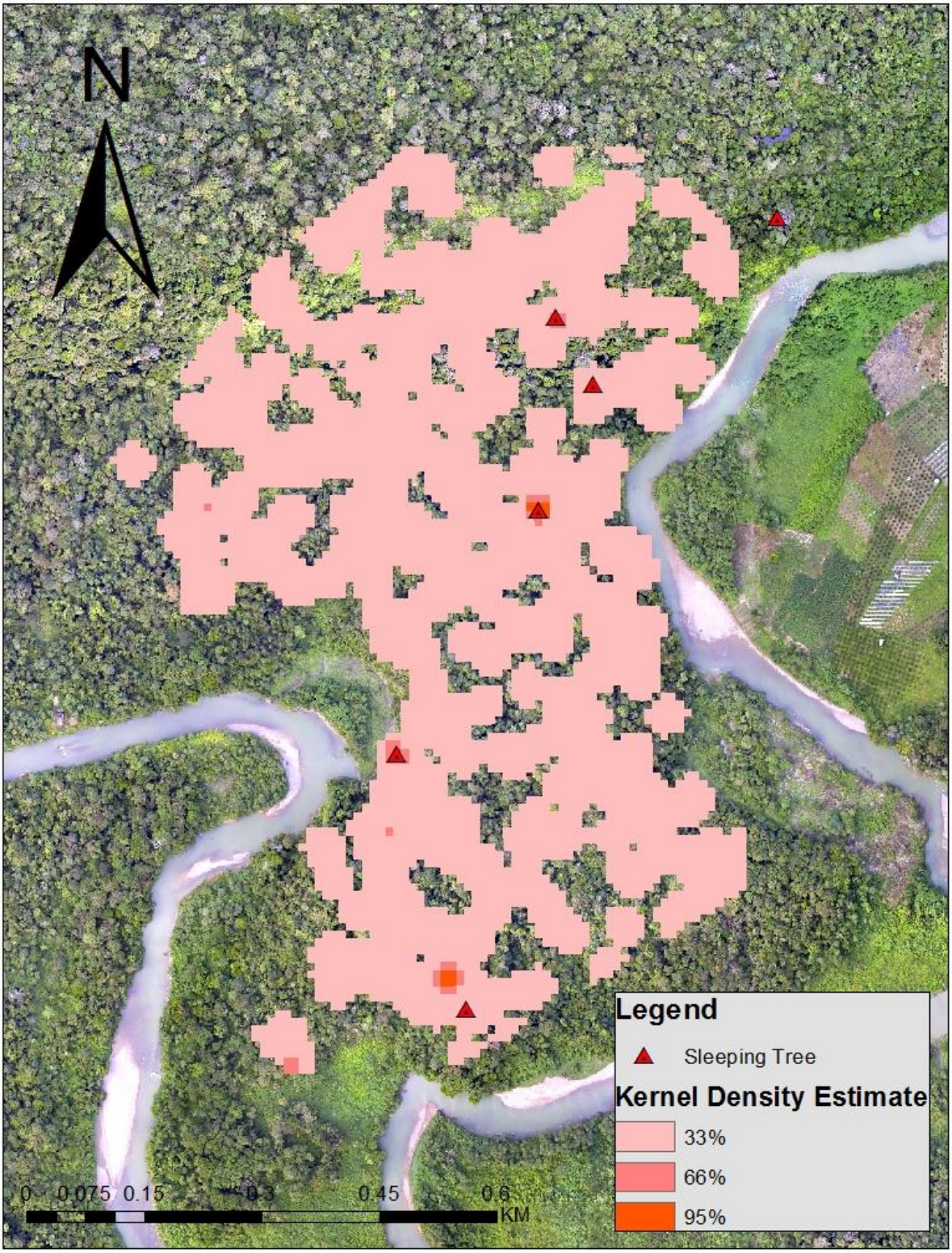


Figure 4.20 Location of Group A's sleeping trees (n = 6) within the home range (April-August) calculated with the Kernel method, subdividing the periphery (33% & 66%) from core areas (95%). The siamang did not use the most northern and most southern sleeping trees seen on the map during the period of this study. The underlying orthomosaic image was obtained from Alexander *et al*. (2018).

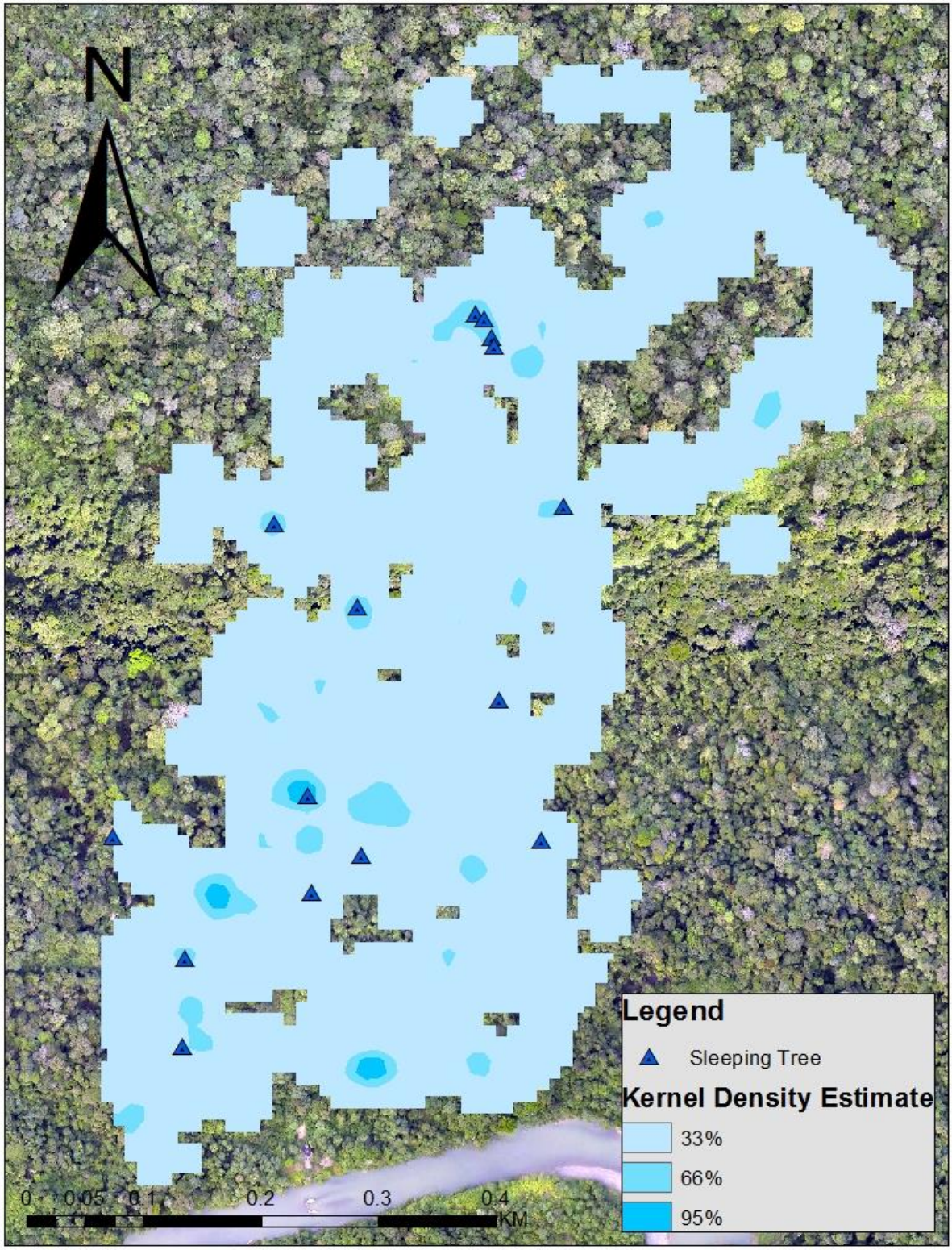


Figure 4.21 Location of Group B's sleeping trees (*n* = 15) within the home range (May-August) calculated with the Kernel method, subdividing the periphery (33% & 66%) from core areas (95%). The underlying orthomosaic image was obtained from Alexander *et al*. (2018).

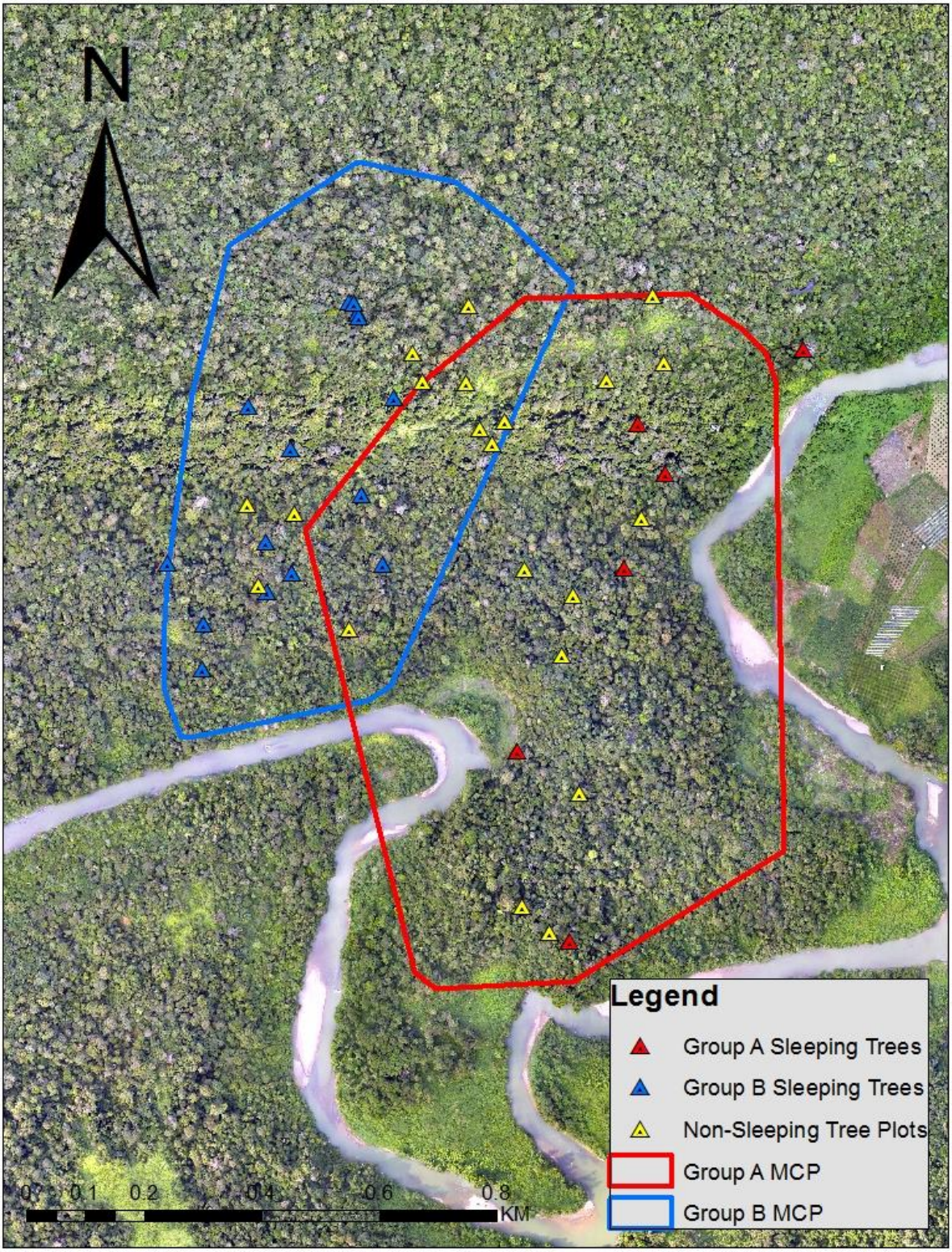


Figure 4.22 Location of sleeping trees and emergent non-sleeping tree plots within the home range of both groups calculated using a minimum convex polygon. The underlying orthomosaic image was obtained from Alexander *et al*. (2018).

5. DISCUSSION

The aim of this study was to identify tree characteristics and forest structures that influence siamang sleeping tree selection. Sleeping trees as well as surrounding trees were compared to tall, emergent non-sleeping trees within the siamang's home ranges. Vegetation assessment of these two tree types and the surrounding forest revealed that siamang actively select trees with specific characteristics, and that the surrounding vegetation impacts their decision. Siamang displayed a specific set of behaviours when it came to retiring to a sleeping tree, choosing trees that were located throughout their home ranges and not restricting them to the core area. Sleeping trees were not positioned near important food resources but may instead have been chosen on a basis of comfort and stability. Sleeping tree re-use was a common occurrence for both the group and the solitary female indicating a more flexible approach compared to other primate species where similar investigations have been carried out (e.g. *Hylobates lar*, <25% of trees were repeatedly used; Reichard, 1998). The results of this study indicate that factors influencing tree selection are not mutually exclusive and that siamang base their decision on various behavioural and ecological aspects.

5.1 Function of sleeping trees

As well as selecting tall emergent trees with broad diameters and large crown areas that were exposed above the mean canopy height, this study confirms that siamang require sleeping trees to have an optimum physical connection with the neighbouring canopy, a lower number of larger branches and to be surrounded by taller trees. Through determining these vegetation characteristics it has been possible to support hypothesis 1a and 1b (although there were no differences between vine and liana load between the two tree types). Siamang depend on canopy connectivity (i.e. tree branches and foliage

to be physically connected) in order to be able to successfully move through the forest and into their desired sleeping locations via climbing or brachiation (Fleagle, 1976). The canopy connectivity value of sleeping trees was still relatively low however (*Mdn* = 12%), compared to the canopy connectivity of surrounding trees in sleeping plots and the canopy connectivity of surrounding trees in non-sleeping control plots (*Mdn* = 60% & 63.75%, respectively). Siamang also actively selected trees to sleep in that had fewer larger branches (branches that were over 20cm in circumference; evident from both Mann-Whitney *U* & GLM statistical analysis) compared to control emergent trees. As well as the tree itself, siamang sleeping trees are also influenced by the surrounding forest and vegetation. Siamang slept in trees that were surrounded by taller trees, with higher boles (with both variables then corresponding to larger crown heights), in comparison to tall emergent trees that were not selected as sleeping trees. The vegetation findings here are comparable to studies on other gibbon species that selected similar characteristics such as tall trees with wide diameters and large crowns above the mean canopy height (*H. klossi*, Whitten, 1982a; *H. lar*, Reichard, 1998; *N. concolor jingdongensis*, Fan & Jiang, 2008; *H. pileatus*, Phoonjampa *et al*., 2010; *N. nasutus*, Fei *et al*., 2012; *H. albibarbis*, Cheyne *et al*., 2012; *H. tianxing*, Fei *et al*., 2017). Here, by measuring additional variables, it was possible to identify other vegetation structures that play a part in sleeping tree choice that have not previously been identified. Phoonjampa *et al.* (2010), compared pileated gibbon sleeping trees to all trees within the gibbon's home range with a DBH ≥40cm that were not used as sleeping trees. A similar method was used in this study by utilising UAV technology that identified emergent trees in a tropical forest (Alexander *et al*., 2018). Here, nineteen trees were identified, with an additional two that were in fact siamang sleeping trees. There were no differences between variables that accounted for the size of the tree, such as height

and diameter, that had been comparable in the pileated gibbon study (Phoonjampa *et al*., 2010). When sleeping trees and emergent non-sleeping trees identified by the UAV were compared, it became apparent that in order to fulfil the criteria of a sleeping tree, trees needed an optimum percentage of canopy connectivity, as well as fewer larger branches.

Siamang are the largest small ape species, up to 1m in height and between 10-12kg in weight (Reichard & Preuschoft, 2016). Their bigger size makes them less agile than other members in their family and they have locomotion and movements more comparable to orangutans than to that of other gibbons when moving through the forest (Fleagle, 1976). Smaller gibbons, such as *Hylobates lar*, are able to jump notable distances (>10m) to move across the canopy (Channon *et al*., 2011). Siamang, however, may not have the physiological adaptations in order to make such progressive leaps between non-connected trees, with Fleagle (1976) reporting siamang jumps rarely greater than 10m horizontally. This may be a driving factor that requires siamang to need an ideal percentage of canopy connectivity and the results of this study showed greater canopy connectivity for sleeping trees compared to control emergent trees, but less so than the surrounding trees. This indicates that an optimum percentage is required in order for siamang to easily recognise and enter/exit a sleeping tree, but as the values recorded were still relatively low, could also be an adaptation to make detectable entry by a predator more difficult. Most predators of primates are crepuscular or nocturnal hunters (Anderson, 1984), and Moynihan (1976) suggested primates are diurnal as a result of this. Anderson (1984) identified tree height, concealment and inaccessibility as important aspects of sleeping trees in terms of avoiding predators. Many primates sleep at higher levels than they are found throughout the canopy during the day (*Alouatta*

palliata, Mendel, 1976; *Callicebus torquatus*, Kinzey *et* al., 1977; *Hylobates klossi* & *Presbytis entellus*, Tilson & Tenaza, 1982) including siamang from the Malay Peninsula (Chivers, 1977) and the siamang in this study. Additionally, sleeping at the terminal ends of branches seems to be a common trait in larger primates including hylobatids (*Symphalangus syndactylus*, Chivers, 1974) and this was observed here. Hypothesis 2aiii is therefore supported. This strategy may reduce predation risks by increasing the chances of detection of a predator through the vibrations of the smaller branches, or by the branches not being able to support both the primate and predator's weight (Jay, 1965). Concealment (or hiding) within vegetation in a sleeping tree is also common throughout a range of primates (*Callithrix humeralifer*, Rylands, 1981; *Cebuella pygmaea*, Soini, 1982; *Callimico goeldi*, Pook & Pook, 1981), although was not observed by siamang.

Cheyne *et al*. (2012) deem predator access routes an influencing factor of agile gibbon sleeping trees. Trees that have a greater number of larger and more stable branches may provide access routes for larger-bodied predators attempting to enter a sleeping tree from the canopy of another tree. Large cats such as Sumatran tigers are still present in the area. Whether tigers have the physical adaptations to be able to climb trees as tall and wide as sleeping trees is unknown, however, other felids such as clouded leopards (known predators of pileated gibbons and black crested gibbons; Fan & Jiang, 2008; Phoonjampa *et al*., 2012) and leopard cats were also seen on cameras in the study area. Other potential predators include snakes; pythons (*Python* spp.) are known by local field guides to be in the area and would have no problem accessing said trees. Sleeping trees were also surrounded by tall trees, with high boles which may be harder to access from the ground. Smaller trees that have low boles, as those seen in control plots, may

provide a platform to access the canopy where siamang sleep, and therefore increase the risk of predation.

The notion that the functional use of a sleeping tree is to avoid predators can be supported by the siamang's behaviour. Siamang always entered sleeping trees before sunset, a common feature documented in other primates, such as tamarins (*Saguinus mystax* & *Saguinus fucicollis*; Heymann, 1995) and titi monkeys (*Callicebus nigrifons*; Caselli *et al*., 2017). In previous gibbon studies, this is thought to be a way to avoid nocturnal predators and here it can be inferred that siamang behave in a similar way (Fan & Jiang, 2008; Phoonjampa *et al*., 2010; Cheyne *et al*., 2012; Fei *et al*., 2012). Hypothesis 2aii is therefore supported; however, siamang did not always move directly to their sleeping position and did not remain still and inconspicuous as predicted. On average there was a lag of five minutes from entering a sleeping tree to reaching their sleeping positions. This is opposed to other studies where primates move quickly and directly in and out of sleeping trees and to their sleeping positions. On three occasions, Group A entered their sleeping tree (A4) relatively early (165-220 mins before sunset) and proceeded to eat the fruit of a liana growing on the tree. Group A often groomed one another and the two males would quibble, while the solitary female would enter a tree and rest near the bole before moving higher up to a sleeping branch. These results indicate that although siamang are actively seeking to avoid predation, they are more flexible than other gibbons. Again, this could be an adaptation influenced by their bigger body sizes. As the largest hylobatids, up to two times the size of their sympatric cohabitants, the lar gibbons (Palombit, 1997), they may be less susceptible to predation, both aerial and terrestrial. Raptors, felids and snakes that target smaller gibbons may have a harder time trying to kill and eat larger siamang. While groups will still need to

consider the risk for juvenile and young individuals, moving quickly and quietly in and out of a sleeping tree may not be a behavioural adaptation siamang have evolved. Black crested gibbons, agile gibbons and Skywalker hoolock gibbons have been shown to leave their sleeping trees after sunrise (Fan & Jiang, 2008; Cheyne *et al*., 2012; Fei *et al*., 2017), whereas siamang in this study left their sleeping trees before sunrise. Similar results were shown in Gittins & Raemaekers' (1980) study of Malay siamang, which had daily activity patterns of ten hours, compared to nine hours of that of lar and agile gibbon. Considering the siamang's more folivorous diet, this is understandable as leaves are less nutritional than fruit and the siamang need to remain active for longer in search of suitable food sources (Gittins & Raemaekers, 1980).

When primates sleep they become less active and less aware of their surrounding environments (Lima *et al*., 2005). In areas such as Sikundur where predator abundance is still fairly considerable, failure to take these necessary precautions when choosing a place to sleep may lead to the ultimate price. Selecting sleeping sites based on safety from predators therefore seems a reasonable behaviour adopted by siamang as indicated from the results presented here.

5.2 Patterns of use and re-use

Siamang did not use as many sleeping trees as expected and frequently used the same trees multiple times and on consecutive nights. From 95 observations across the two siamang groups, 19 sleeping trees were identified, with an additional two identified outside of this study period by a previous researcher. Unlike hypothesised, the focal siamang in this study have regular sleeping trees, a feature undocumented in other hylobatid studies, and one that goes against a theory of predator avoidance. Hypothesis

2ai is therefore rejected. In Reichard (1998) and Cheyne *et al*., (2012) gibbons used many sleeping trees, infrequently using the same tree more than once during the study period and rarely or never on consecutive nights. Using a sleeping tree multiple times increases predictability, and this coupled with a build up of odour from defecation could lead to increased risks of predation. There are however, explanations as to why siamang may re-use sleeping trees in such ways.

Siamang are the only species of hylobatid to live sympatrically with another member of the same family. Lar gibbons are present in northern Sumatra while agile gibbons are found centrally and in the south. In the Sikundur area, lar gibbons are estimated at a density of 1.19-3.56 groups/km^2 (Hankinson, 2017) and were regularly heard and occasionally seen within the siamang's home range. Lar gibbons are known to have dozens to hundreds of sleeping trees (Reichard, 1998), but their ranging areas are larger than that of siamang, 40 hectares as opposed to 26 hectares (Gittins & Raemaekers, 1980), therefore increasing the amount of potential sleeping trees spatially. Siamang, with their more folivorous diets, also have shorter daily travel distances, 0.8km/day compared to lar gibbons 1.4km/day (Gittins & Raemaekers, 1980), as the amount of folivorous food is essentially unlimited in the forest, and they do not need to travel as far. These factors spatially decrease the amount of suitable sleeping sites and may explain the small number of overall sleeping trees and the high rate of re-use. As well as these behavioural and distributional differences, the area's history may also influence primate sleeping tree selection. Sleeping sites may be a limiting resource and in yellow baboons (*Papio cynocephalus*) sleeping trees were as limiting as food and water (Washburn & Devore, 1961; Washburn & Hamburg, 1965). Sikundur is a degraded forest that was selectively and mechanically logged for a 30-year period prior to the 21st

centaury. Selective logging at Sikundur removed the largest and most commercially valuable trees from the area whilst mechanical logging cleared large areas of vegetation, both causing severe damage to the forest's canopy (Priatna *et al*., 2006). Results from vegetation analysis showed that canopy connectivity is an important factor for sleeping tree selection, as is the height of surrounding trees. Logging of both kinds may limit sleeping trees as a resource by removing these vegetation qualities from the forest so that siamang are unable to move through the canopy or select trees that have the right characteristics for predator avoidance. Instead of choosing trees that are 'lower quality' for their sleeping requirements, they re-use the ones that provide safe and stable sites. Group A's sleeping tree use was extremely low with a total of six known sleeping trees, compared to 15 for the solitary female and the many more trees used by siamang in Batang Toru (M. G. Nowak, *pers. comm*. Aug. 2018), but may be explained by the location of their home range within the forest. Bordered by an ex-logging road to the north (which is still frequently used by local villagers on motorbikes to access the Sikundur camp and river), and the Besitang river on all other sides, Group A's home range is extremely accessible to humans, and has potentially suffered the most amount of degradation, both historically and presently. Figure 3.2 shows areas on the Sikundur peninsular that have <25% tree cover as well as illegal forest loss since 2000 near to where Group A reside. Life in a group demands more resources and therefore requires bigger, more stable trees with larger crowns and more small branches to be able to support their numbers, which the solitary female siamang did not need. Hypothesis 1c is therefore supported. This, coupled with the accessibility of the area could impact siamang sleeping trees by removing the groups' necessary requirements, leading to a lower number of total sleeping trees used. As previously discussed, their larger body sizes may also affect the use of regular sleeping trees. Whether a tree has been recently

used to sleep in may not be a driving factor when it comes to selecting a place to sleep, and that the vegetation characteristics siamang require are enough to influence the decision.

The distance to important food sources may be an influencing factor on sleeping tree location and use because it incorporates travel routes and foraging strategies (Pontes & Soares, 2005; Tsuji, 2011; Schneider *et al*., 2013). Having multiple sleeping sites that are widely distributed throughout the home range can optimise time budgets in relation to feeding (Caselli *et al*., 2017). Siamang in this study, however, did not use sleeping trees based on their proximity to feeding resources, i.e. fruiting trees. As mentioned, siamang are the most folivorous amongst the hylobatids. Their diet compromises 48% leaves compared to 29% in the lar gibbon and 39% in the agile gibbon (Gittins & Raemaekers, 1983). They therefore do not need to position their sleeping sites near to fruiting trees as leaves in a tropical rainforest are essentially an unlimited resource, giving siamang more flexibility when it comes to feeding and foraging in relation to sleeping locations. Although forest dwelling primates tend to sleep close to areas where they have been feeding in the late afternoon (Roonwal & Mohnot, 1977; Rodman, 1979), Gittins (1982) found that this was not always the case of monogamous and terrestrial groups, two behaviours displayed by siamang. Hypothesis 2b is therefore rejected.

Primates may select places to sleep based on comfort and stability. Pygmy marmosets (*Cebuella pygmaea*) did not sleep in feeding trees to avoid being disturbed by nocturnal feeders (Rudran, 1978). Kloss gibbons (*H. klossii*) avoided trees with epiphytes as these were hosts to biting ants, which disturbed sleep (Whitten, 1982a). Chimpanzees (*Pan*

troglodytes schweinfurthii) choose locations with appropriate fibrous wood to build their nest so branches do not spring back when sleeping (Goodall, 1962). Siamang slept mostly at the end of bare branches and although in this study sleeping locations were not categorised into further detail, it was possible to deduce which sleeping trees provided a better quality of sleep based on the number of rests that day. When siamang were more tired and rested more throughout the day, they retreated to specific trees, potentially indicating that these trees provide a higher level of comfort and stability to be able to get more sleep that night. Comfort and stability is probably a secondary consideration when choosing when to sleep (Anderson, 1984), and the risk of predation may also plays a part; siamang may get a better quality of sleep in trees where they feel more safe from predators. This result suggests siamang compare different sleeping sites from a comfort point of view before making a selection, and thereby supporting hypothesis 2c.

5.3 Home ranges and sleeping tree locations

In Chivers (1972) siamang sleeping trees were in the core of the home range, i.e. the most intensively used areas. In this study, core areas were not predominant, and siamang used the extent of their home ranges relatively evenly. Sleeping trees were in almost all areas of a siamang's range, with most trees located in the central regions, few at the edges, and a couple in the overlap area of Group A and Group B (Fig. 4.22) therefore disproving hypothesis 3a. The finding from Reichard (1998) indicated that lar gibbons had around 20% of their sleeping trees in overlapping ranges with other groups and similar results have been shown in pileated gibbons (Phoonjampa *et al*., 2010). The opposite was observed in the Cao Vit gibbon where they actively avoided sleeping trees in overlapping areas (Fei *et al*., 2012). Selecting trees at the edge of the home range

may be an adaptation for range defence but may not be the most logical location to sleep considering the territorialism of gibbons and siamang, which can sometimes be fatal (Palombit, 1993; Smith, 2007). The historical disturbance of the site may leave no other choice for sleeping trees with ideal characteristics except in overlapping areas, and the densities of siamang at Sikundur (0.40 – 2.11 groups/km^2; Hankinson, 2017) implies that encounter rates at sleeping trees may be uncommon. Competition for the best sleeping site was, however, witnessed on several occasions. During the study period, intra-specific competition was observed when a solitary female siamang was seen sleeping in the most northern sleeping tree (A5) of Group A. Inter-specific competition was also witnessed when a solitary female lar gibbon slept in a sleeping tree of Group B, and on at least five occasions Thomas' langurs and pig tailed macaques were seen in sleeping trees of both siamang groups. Sleeping sites may be limited resources (Anderson, 1984), with some primate species sharing sleeping sites with different groups (*Nasalis larvatus*, McDonald, 1982; *Semnopithecus entellus*, Hrdy, 1977; *Aotus nancymai* & *Aotus vociferans*, Aquino & Encarnación, 1986), with other species (*Aotus vociferans* with other species of mammals, Puertas *et al*., 1995) or with the same species (female *Microcebus murinus*, Radespiel *et al*., 2003). As Sikundur has a history of disturbance, sleeping sites here should be considered a limited resource and therefore competition is expected. As indirect competition was observed both between and within species, hypothesis 3b is supported.

5.4 Project caveats and limitations

This project was limited by various factors that should be considered when understanding the results presented in this thesis. One of the main caveats not accounted for during the study was the possibility of seasonal bias, as data were collected between

April and August only. Sumatra has two seasons one being a drier period between May and September, with the wet season beginning in October, which could affect siamang behavioural ecology. Seasonal variation drives the phenology of fruiting and flowering plants that the siamang forage on throughout their home range. At differing times of the year, siamang may use areas of their home ranges at different intensities and may adjust their travel routes due to the presence of fruit. Although a relationship between sleeping trees and proximity to fruiting trees was not established in this project, had data been collected across the full year, a correlation may have been established. In addition, Group A had regular sleeping trees and were known to have two sleeping trees (identified by a previous researcher) that they did not use during the period of this study. Had data collection continued for longer, and across the changing seasons, observations of sleeping tree use in these trees may have been recorded, thereby extending the data set.

Another aspect to consider is the sample size in this project. Data were recorded on one family group and one solitary female siamang, as these are the only habituated hylobatids in the area. However, their behaviour should not be considered a full representation of the wider siamang population. Siamang in the extended areas of the Leuser Ecosystem, elsewhere on Sumatra, and on the Malay peninsula may have different sleeping requirements depending on the area's disturbance history, and the siamang's local ecological niches and behavioural adaptations. Furthermore, the frequency of sleeping tree use across both groups must be considered under-sampled. This is because data on sleeping tree use was not recorded every evening during the study period. Siamang may therefore have additional sleeping trees that were not identified during this research, however, as siamang follows were for 3-5 consecutive days throughout the duration of the project, and the number of sleeping trees reached

asymptote, the likelihood of unidentified sleeping trees is low. Furthermore, it was also difficult to be certain that the emergent trees identified within UAV data (from Alexander *et al*., 2018) were not sleeping trees for the siamang. Two emergent trees identified from said study were in fact regular sleeping trees for the siamang, meaning that the other trees identified within and without the focal siamang's home ranges may also be sleeping trees for other siamang groups or other species of primates, particularly lar gibbons. To determine whether emergent trees identified from the UAV data are used as sleeping trees, the project would have benefitted from longer monitoring, across more siamang and even lar gibbon groups within the extended Sikundur area shown by the aerial photographs. Expanding the study in such a way, however, requires substantial time and funding resources, which were both limiting factors in this project.

When recording the data for the vegetation plots, the values displayed for tree height may not be wholly accurate and instead should be taken as a scientific estimate. This is because a range finder, where a laser reflects back to an optical viewer from a distant object to determine height, was used in an environment where dense foliage from the canopy and undergrowth was the norm. The density of leaves, trees and branches made it extremely difficult to target the precise location of the top of the tree, and after some preliminary trials in the field, it was decided that the angle function would be used instead. This method provided more accuracy as the researchers would aim the range finder to the point where they '*believed'* the top of the tree to be and then the height was worked out with a mathematical equation. This was more effective than attempting to point the laser to the actual tree top, however, it had its own limitations as it required the distance from the tree to the range finder to be recorded, which, in a tropical forest with gradients of terrains, often proved difficult. Nevertheless, observational bias was reduced to a minimum by having the same researcher use the rangefinder to measure

tree height throughout the whole of the data collection. To rectify this issue further and in future studies, it may be functional to categorise heights in five- or ten-metre categories, as an absolute accurate measurement, in this instance, would be difficult to obtain.

5.5 The future

None of the previous research on hylobatid sleeping trees and sleep related behaviour in the wild has focused on the gibbons of Sumatra, which is home to three endangered species (lar gibbons; agile gibbons; siamang). As human pressures mount on already disturbed tropical forests, it is important to understand how sensitive species such as primates respond to these modifications in an attempt to conserve dwindling populations. This study provides the first attempt at documenting what sleeping trees are selected by siamang and what their behaviour tells us about this selection. To improve the quality of the results presented here, further research is necessary to fully understand siamang habitat use, specifically where forest structure is concerned. In this study, siamang re-used sleeping trees more frequently then predicted, a feature rarely documented amongst hylobatids. Whether this is a common behavioural trait for siamang across Southeast Asia is unknown and extending studies of siamang sleeping trees in less degraded areas of Leuser, elsewhere in Sumatra and across the Malay peninsular, may provide interesting comparison; do siamang in less degraded areas increase their number of sleeping trees, or are sleeping trees restricted by the siamang's smaller home ranges overlapping with other gibbons, their larger bodies, or their more folivorous diets?

Behavioural studies of primates benefit from larger sample sizes over longer durations. This study was limited by both of these factors. At Sikundur, only one group and one solitary female are habituated to human presence. To increase our understanding of habitat use, it would be beneficial to habituate more siamang, as well as groups of lar gibbons. Groups of both species were regularly heard and occasionally seen, indicating that Sikundur has a healthy population of hylobatids. The sleeping trees of lar gibbons has already been documented (Reichard, 1998), but this study was in an area that did not overlap with siamang home ranges. As siamang are the only member of Hylobataidae to occur sympatrically with other gibbons, this could be an important factor for sleeping tree selection influenced by inter-species competition. Studying siamang and gibbons that occupy the same habitat may provide further insight about the behavioural ecology of these at risk species, leading to more efficient conservation management. As Sikundur has experienced a gradient of disturbance, this would be the perfect opportunity to study how species, within and outside of primatology, respond to forest degradation. A project such as this would benefit form long-term monitoring, however this requires substantial funding sources, which, along with time, were limiting factors in this project.

5.6 Implication for conservation

Deforestation is considered the largest contributor to biodiversity loss (Brun *et al*., 2015). In Indonesia, only 3.8% of original primary forest remains (Cheyne *et al*., 2012), with intensive and selective logging practises altering the forest's arrangement (Priatna *et al*., 2006). Between 1985 and 2010, 14.9 million hectares of forests were lost on the island of Sumatra (Gaveau *et al*., 2007; Abood *et al*., 2015). In order to protect species that are sensitive to habitat modification, local and national authorities must take critical

action to reduce large-scale land clearance and prevent illegal deforestation. This study is the first of its kind on the island of Sumatra and the first to be conducted on siamang. The results revealed that siamang are able to adapt their sleeping behaviours to live in degraded forests and tolerate different levels of disturbance. Nevertheless, the future is still uncertain for these primates. With slow reproductive rates and late age of maturity (Bartlett, 2007), recovery of reduced populations cannot be guaranteed. Siamang are listed as 'Endangered' on the IUCN Red List with a declining population trend (IUCN, 2017b), with gibbon populations having suffered a dramatic decline in the last 40-50 years, the main cause being habitat destruction (Cheyne, 2009; Bodmer *et al*., 1991). Governments of those countries where gibbon are present must provide the necessary education and alternatives to deforestation, illegal trafficking and hunting to avoid further decimations (Cheyne, 209). Without rigid and enforced conservation efforts, healthy siamang populations, such as those at Sikundur, are expected to suffer local scale extinctions.

6. CONCLUSION

Tropical forests are being removed at an alarming rate, disrupting carbon cycles and increasing global temperatures. This disruption and loss of important habitat requires immediate scientific research if we are to better understand how species such as primates adapt to these changes within their ecosystem. Sumatra hosts some of the world's richest and most diverse ecosystems on the planet but has gained renewed interest because of its increasingly high deforestation rates (Page *et al.,* 2002; Gaveau *et al.,* 2009). Siamang are unique among the hylobatids, yet remain relatively under-studied and their behavioural ecology is not fully understood. There are many studies detailing primate sleeping sites in depth, with most indicating that primates choose sleeping sites based on a theory of antipredation, comfort, and distance to importance food resources (Anderson, 1984).

The results of this study were clear; siamang slept in tall emergent trees with broad diameters and large crown areas that were exposed above the mean canopy height, as other gibbons have been shown to do, and indicating sleeping trees are chosen to avoid predation. In support of this, siamang need sleeping trees to have a lower number of larger branches and to be surrounded by taller trees. Siamang also require sleeping trees to have an optimum physical connection with the neighbouring canopy, a forest characteristic that has been untested in the past, but one that may be necessary for understanding movement in and out of sleeping trees for larger bodied primates. Sikundur has a gradient of disturbance that provides a unique opportunity to study how animals have adapted to anthropogenic pressures. The area's historic disturbance may explain why the siamang at Sikundur re-use sleeping trees as often as they do, and

shows siamang are more flexible at withstanding disturbances than previously thought. As this kind of disturbance has caused sleeping trees to become a limited resource in the area, competition between and within species was observed. The siamang's more folivorous diet means that they do not require immediate access to fruiting trees and they therefore did not strategically position their sleeping sites near important food sources. Instead, sleeping trees were chosen based on the number of rests, indicating comfort is an important influence.

This study is the first to assess sleeping behaviours and forest structure relating to sleeping trees used by siamang and the first sleeping site study to be undertaken on Sumatra on any primate other than orangutans (Sugardjito, 1983). Even though the siamang here have shown flexibility to a degraded forest and have survived a period of disturbance, as anthropogenic pressures mount of Sumatra's forests, primate populations, including that of siamang, are expected to continue to decline.

7. LITERATURE CITED

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